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May 1976

PHOSPHATE REDUCTION AND RESPONSE OF PLANKTON POPULATIONS IN KOOTENAY LAKE

by

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ABSTRACT

The purpose of this research project was to determine the effects of reducing by 90 percent the soluble inorganic phosphate input to Kootenay Lake, British Columbia, Canada, a significant link in the Columbia River system governed by United States-Canadian treaty. Measurements on temperature, transparency, inorganic and organic phosphate, nitrate, ammonium, chlorophyll *a*, copepods, and cladocerans were made during 1971-75, and compared with observations made for three years prior to phosphate reduction in 1969. Only a slight decrease in chlorophyll occurred, although there were important changes in species composition. Total zooplankton levels were not affected, however one genus (*Daphnia*) has virtually disappeared. Data indicate that primary production in the lake was nitrogen limited prior to 1969, phosphate limited two years later. These changes may also be related to the completion in 1972 of Libby Dam in Montana, upstream from the lake on the Kootenay River. An overview of the results is reported, with detailed accomplishments reported in Parker [1,2,3,4,5,6] incorporating the unpublished work of J. E. Cloern, J. R. Davis, J. R. Hargis, and K. G. Taylor.

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SECTION I

INTRODUCTION

The effects of an increase in the nutrient budget on lakes have been well documented in several cases (see for example Hasler[7], Edmondson et al.[8], Edmondson[9], Beeton[10, 11], Verduin[12]). There have been fewer reports of the response by an enriched lake after reduction in the nutrient income (Edmondson[13, 14], Ahlgren[15], Malueg et al.[16]). Kootenay Lake, a large, generally oligotrophic lake in southeastern British Columbia, Canada, received significant quantities of inorganic phosphate via the Kootenay River from 1953 until 1969. This material originated primarily from the activities of a fertilizer plant located on a tributary of the Kootenay River near Kimberley, British Columbia. Early in 1969 there was a large reduction (80-90%) in the amount of phosphate being put into the river and thus into the lake.

Prior to phosphate reduction, Taylor[17] and Parker[1] conducted a limnological study from 1966 until 1969, emphasizing nutrient levels and plankton densities. About the same time, Fillion (unpublished) focused attention on the phytoplankton composition. His samples have subsequently been examined by Northcote et al. (unpublished) at the University of British Columbia. Zyblut[18] reviewed long-term changes in the zooplankton population of Kootenay Lake, and Northcote[19] provided a historical account of the salmonid fishery as it related to human activities and nutrient loading. Further study was begun in 1971 and continued through May 1975. Results from the second period will be compared with those given by Taylor[17], focusing largely on changes in nutrient concentrations and plankton populations. It also should be pointed out that changes caused by reduced phosphate income have been compounded by completion of Libby Dam, located several hundred kilometers upstream on the Kootenay River in Montana. Shortly after leaving the Lake, the Kootenay River joins the Columbia River, providing about 30 percent of the total low flow at that point. The general drainage characteristics of Kootenay Lake, as well as nutrient loading before and after 1969, are summarized in Table 1.

Table 1. DRAINAGE CHARACTERISTICS AND NUTRIENT LOADINGS FOR KOOTENAY LAKE

Drainage Characteristics	
Drainage Basin (km^2)	45,669
Lake Surface Area (km^2)	417
Annual Inflow (m^3)	26×10^9
Lake Volume (m^3)	40×10^9
Retention Time (days)	566
Lake Mean Depth (m)	96
Nutrient Loadings	
Nitrate - Nitrogen ($g/m^2/yr$)	
1966-69	0.45
1971-74	0.48
Ammonium - Nitrogen ($g/m^2/yr$)	
1967-69	0.25
1971-74	0.18
Phophate - Phosphorus ($g/m^2/yr$)	
1966-69	0.68
1971-74	0.051

SECTION II

CONCLUSIONS

Seasonal flow patterns of the Kootenay River have been altered considerably by the completion of Libby Dam in 1972. The peak values during the spring run-off period in late May and early June have been reduced approximately 50%, with the balance of the flow being distributed over the summer period. Temperatures in the lake are somewhat lower than before the construction of the dam, and the transparency of the lake has been increased by a factor of two during late spring and early summer, coincident with lower volume flows.

Soluble inorganic phosphate entering the lake has decreased approximately 90% since 1969. There has also been a concurrent decrease in the soluble organic phosphate fraction as well as in the particulate phosphate. The soluble organic fraction has, however, not decreased as much as the inorganic fraction. Furthermore, the decrease in the particulate fraction can be attributed largely to a decrease in silt load brought about by reduced flows of the Kootenay River. Nitrate and ammonium concentrations have changed little since 1969, although reductions during the summer period due to algal growth no longer appear to be limiting to the phytoplankton populations. Rather phosphate has become the nutrient of prime consideration.

Chlorophyll *a* levels in Kootenay Lake have been reduced 10-15% as a result of reduced phosphate input and somewhat lower temperatures. There has been a change in the species composition of the phytoplankton, with diatoms playing an increasingly important role relative to blue green algae. *Daphnia* has been virtually eliminated from Kootenay Lake for reasons that are unclear. Preferential feeding by landlocked sockeye salmon in a more transparent lake could be responsible. This would of course require that *Diaphanosoma* not be preyed upon heavily since this genus has become the dominant cladoceran in the lake. Larger copepod populations could be brought about by reduced grazing pressure by *Daphnia* on important food items like *Cyclotella* and *Cryptomonas*.

SECTION III

RECOMMENDATIONS

Although phosphate input into Kootenay Lake has been decreased from 0.68 to 0.05 g/m^2/year, attempts to predict the consequences on plankton populations have only been partially successful. The differential equations used to simulate the system suffer from lack of an adequate hydrodynamic component, as well as reliable estimates of essential parameters. If the model developed for this lake is to be applied further, or to other lakes, inclusion of a well-defined hydrodynamic sub-model is recommended. In addition, rate constants for phytoplankton populations should be measured in the field, including dependence on light intensity, temperature, and nutrient concentrations. Other types of mathematical models (e.g. multivariate regression) should also be investigated to improve prediction accuracy needed for sound management.

SECTION IV

FIELD OBSERVATIONS AND LABORATORY ANALYSES

METHODS

Sampling stations on Kootenay Lake were the same for 1971-74 as those used by Taylor[17], with the exception that Station 3 was discontinued in 1973 (Figure 1). Velocity of river input was measured during 1974-75 at Station 1 with an Ott current meter at 1 m, and at Station 2 by means of drogues. Temperature and light penetration were measured by Whitney underwater instruments. Readings were taken at 1-m intervals from the surface to 10 m at Stations 2-5, and to 5 m at Station 1.

Zooplankton samples were collected at Stations 2-5 using a Clarke-Bumpus sampler with a number 10 nylon net towed at approximately 3 km.p.h. Two samples were collected at each station and each of three depths (1, 5, 10 m). The samples were preserved in formalin and counted subsequently in the laboratory. Five 1-ml subsamples of a known dilution of the original sample were removed by piston pipette and counted on Sedgewick-Rafter cell. The density of a given zooplankton species was then calculated as follows:

$$\text{Number/liter} = \frac{\text{total no. in subsamples}}{5} \times \frac{\text{vol. of dilution}}{4 \times \text{no. of revolutions}} \qquad (1)$$

Water samples were collected at each station by Kemmerer bottle. At Station 1 two samples were taken at 1 m, and at Stations 2-5 two samples were collected at each of the three depths. Two subsamples of known volume (300-500 ml) from each original sample were filtered using a 0.45μ membrane filter (Gelman, 47 mm dia.). One filter was analyzed for particulate phosphate, and one analyzed for total chlorophyll *a*.

The chlorophyll *a* concentrations were measured by soaking the filter in 10 ml of 100% methanol for 3-4 hours, then reading the optical density at 660 nm with a 1 cm path length. To convert the optical density to chlorophyll *a* concentration in μg /liter, the optical density was multiplied by 13.9 x vol. of water filtered x vol. of solvent used (10), as suggested by Talling and Driver[20].

The phosphate concentration was measured using the method of Strickland and Parsons[21]. Nitrate was analyzed using the phenoldisulfonic acid method of APHA, AWWA, and WPCF[22]; ammonia determinations were made using the method of Solorzano[23].

Samples ordinarily were collected weekly during the summer, biweekly in the spring and fall, and monthly in the winter. Mean values over 10 meters will be used as the basis for subsequent discussions of all variables considered.

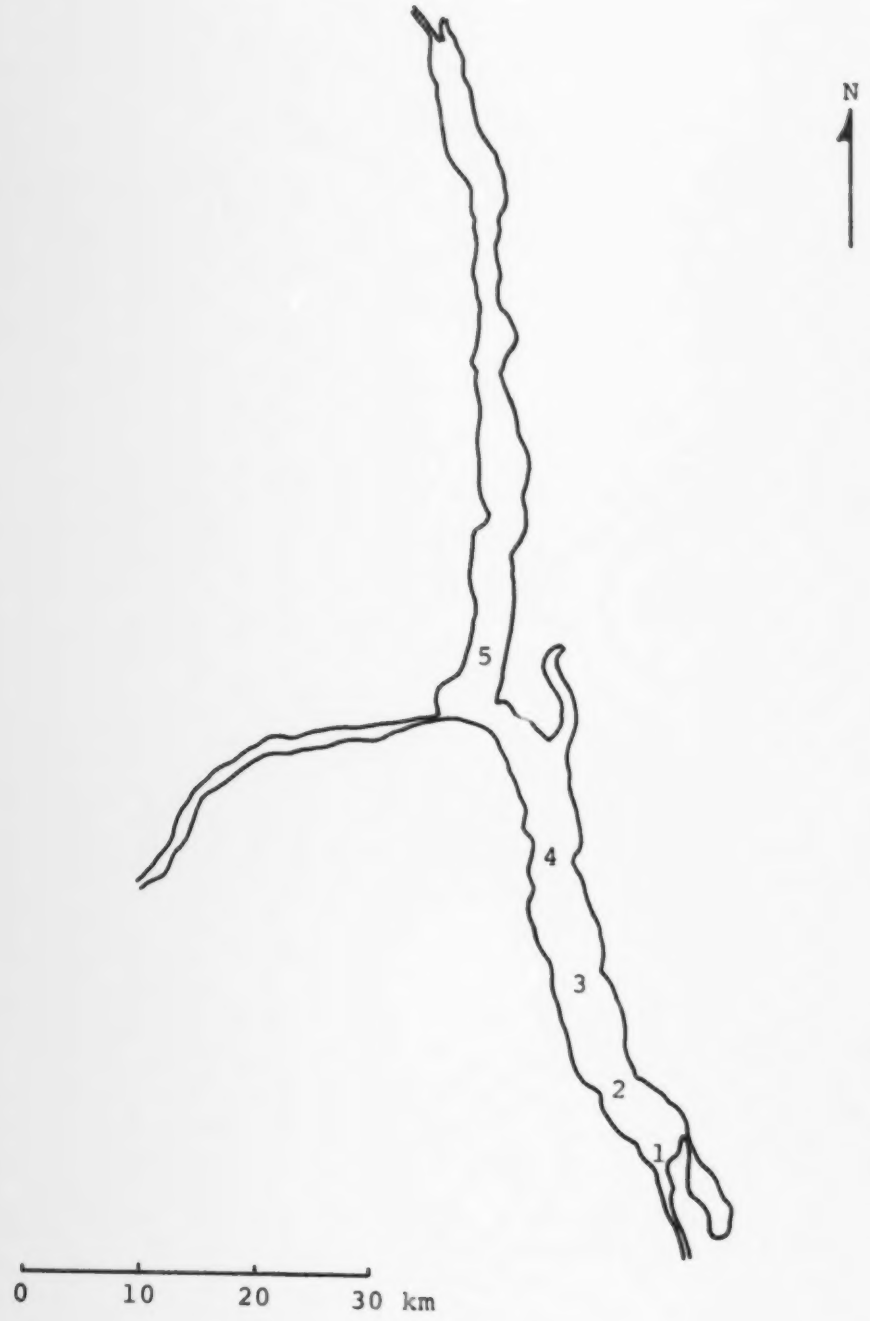

Figure 1. Sampling locations on Kootenay Lake

PHYSICAL CHARACTERISTICS

River Flow

The seasonal pattern of flow of the Kootenay River was altered considerably following the completion of Libby Dam in 1972 (Figure 2). During 1966-1969, peak flow occurred early in June and was approximately two million liters per second. In 1972 the peak was approximately 1.6 million liters per second, less than 0.5 million liters per second in 1973 and about 1.2 million liters per second in 1974. Attempts to disburse accumulated water from the reservoir behind Libby Dam over a longer period (and more gradually) were moderately successful.

This new flow pattern has had a considerable effect on the temperature regime of the lake, as well as on the transparency of the water. Nevertheless the water flows northward along the eastern shore of the lake from the point of entrance of the river at the south end. In fact, this water may travel all of the way to the north end of the lake, where it mingles with water entering in the Duncan and Lardeau Rivers, before moving southward and out through the west arm.

Temperature

Water is released from behind Libby Dam at various depths below the surface of the impoundment in order to maintain acceptable temperatures in the Kootenay River. The fundamental seasonal pattern has not been altered in Kootenay Lake, although there has been a small decrease in mean values (Figure 3). Recall that Station 1 is located at the point where the Kootenay River enters the lake, and that Station 2 through 5 are distributed over the south half of the lake.

Transparency

Figure 4 illustrates well the effect of changing the seasonal flow pattern on the transparency of water in and entering Kootenay Lake. The suspended silt load in the river (Station 1) has been reduced markedly by lowering peak flows. This has had a pronounced effect on the extinction coefficients for the upper 10 meters as is clearly shown in Figure 4. This reduction in turn has altered the seasonal growth pattern of the phytoplankton. Prior to 1972, Kootenay Lake typically had a spring bloom followed by substantial reduction during June and another bloom in August and September. Since 1972, phytoplankton levels in the lake have been more evenly distributed throughout the growing period. Extinction coefficients in the lake (on a per

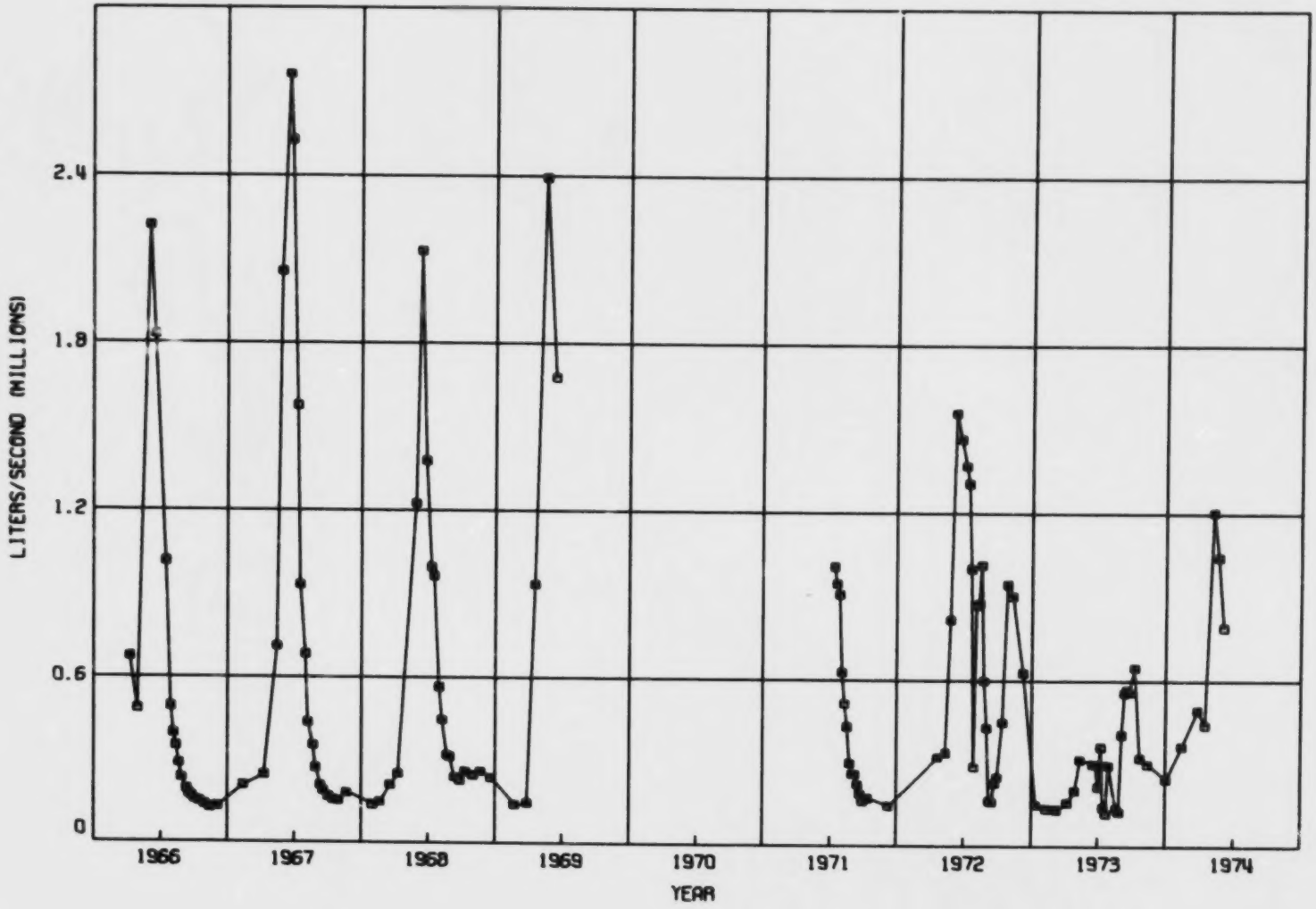

Figure 2. Flow of the Kootenay River at Station 1.

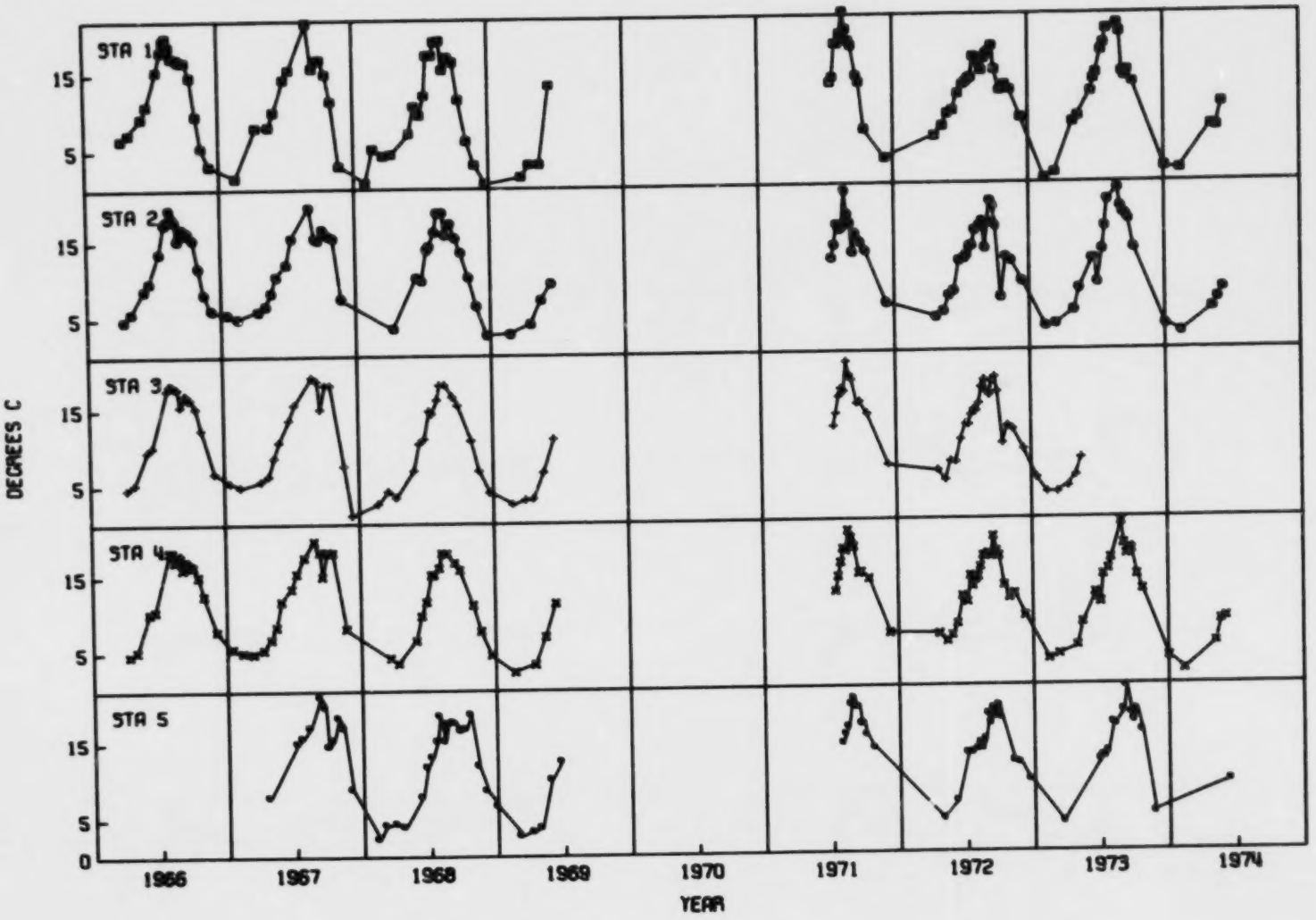

Figure 3. Mean temperatures at Stations 1-5.

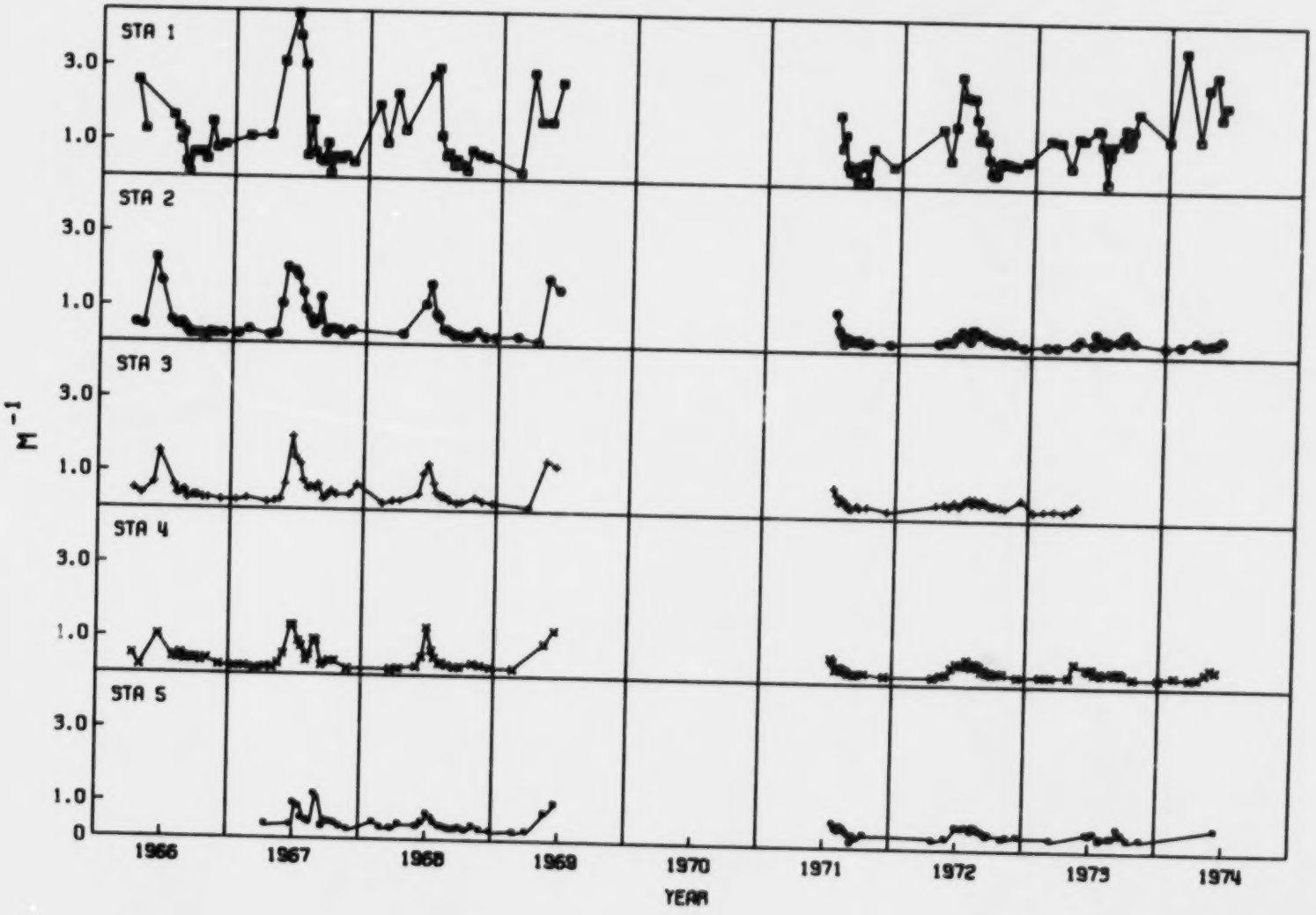

Figure 4. Extinction coefficients.

meter basis) frequently reached 2.0 in June; since 1972 values rarely, if ever, exceed 1.0. This means, of course, that the depth to which one percent of the surface light is transmitted during the most turbid periods has been increased from about two meters to over four meters.

NUTRIENTS

Phosphorus

Prior to 1969 the amount of inorganic phosphorus entering Kootenay Lake at Station 1 ordinarily exceeded a concentration of 12 micromoles per liter (μM/l) during the winter months. Since 1969, concentrations in entering river water have not exceeded 2 μM/l (Figure 5). Although concentrations were obviously low during the winter months, maximal daily inputs occurred during periods of peak flow. For example, about 15 metric tons entered the lake on 30 May 1966. Following input reduction, a maximum value of 0.75 metric tons entered on 20 May 1972. Average entrance over the year has been reduced approximately 10 fold, and mean values in the lake have been reduced from approximately 3 μM/l to 0.3 μM/l. The amount of soluble organic phosphate is shown in Figure 6. This quantity does not appear to change significantly during the year, although there has surely been a reduction from about 1 μM/l prior to 1969 to about 0.2 μM/l since. Note that the inorganic phosphate pool in the lake is reduced during the summer period of peak algal growth, particularly during the period of 1971-1974. Prior to 1969, the only significant summer depressions occurred in 1966 and 1967. Particulate phosphate (Figure 7) is composed of phosphate adsorbed on silt particles as well as phosphate incorporated in living organisms. A review of the seasonal distribution for this variable indicates that the highest levels are coincident with peak river flow, thereby suggesting that much of the particulate phosphate is in fact adsorbed material. Unfortunately no attempt was made to distinguish between particulate phosphate in living organisms from that adsorbed to silt particles and, consequently, one cannot use the seasonal distributions as indicative of plankton population fluctuations.

Nitrogen

The highest nitrate concentrations in the Kootenay River occur during winter and spring. These high levels are reflected in values measured at Station 2-5. As with phosphate, maximum total

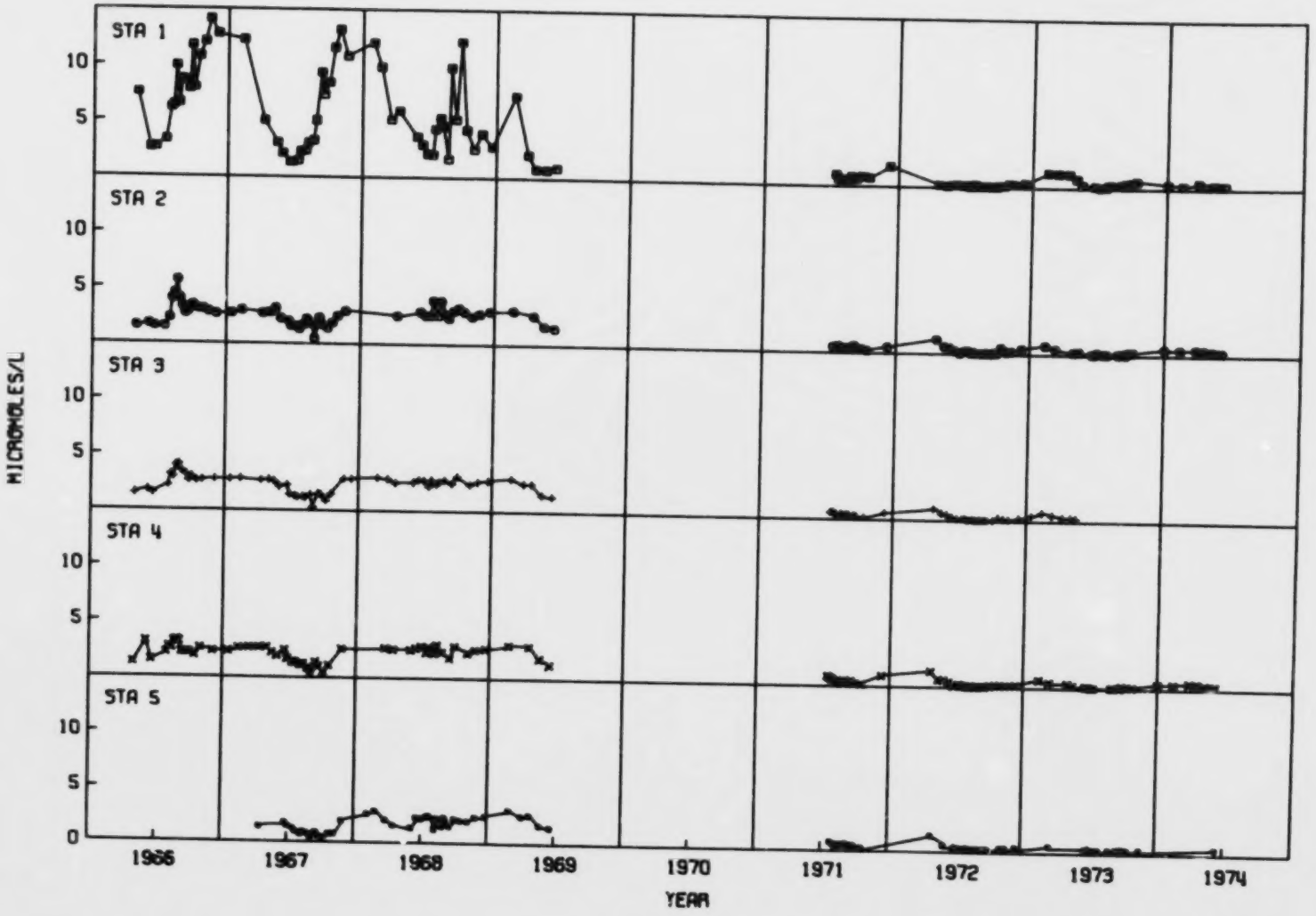

Figure 5. Soluble inorganic phosphate concentrations.

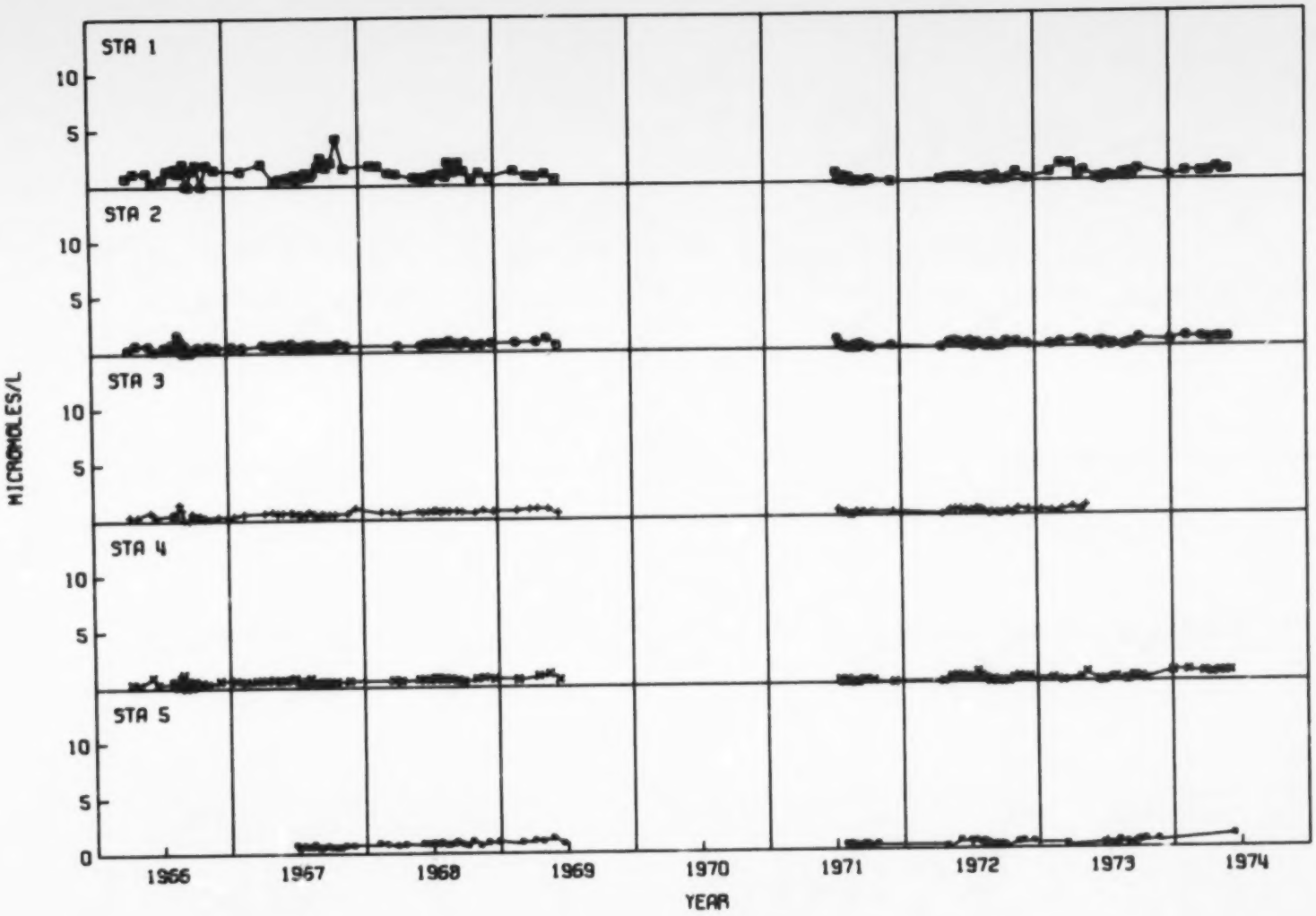

Figure 6. Soluble organic phosphate concentrations.

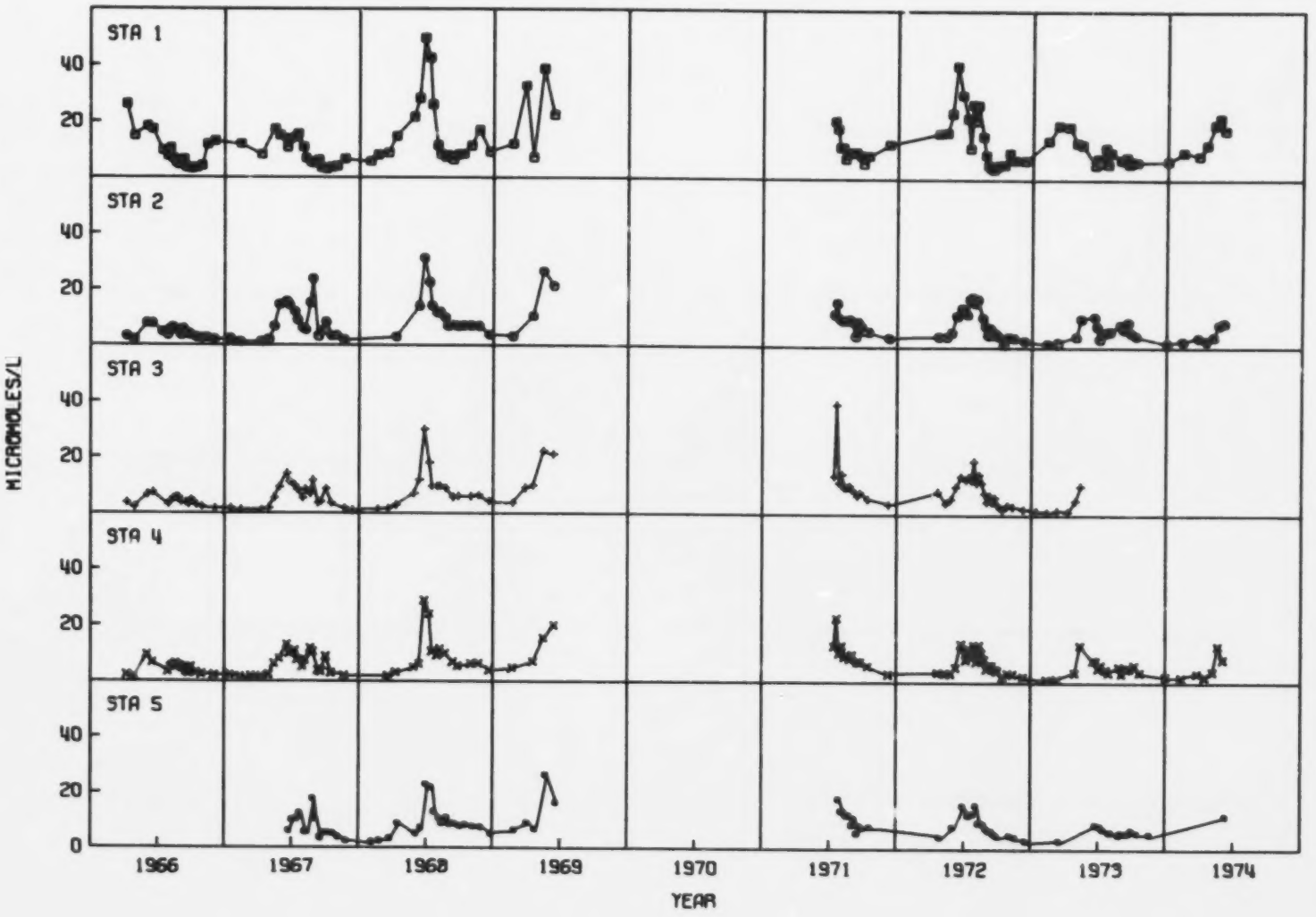

Figure 7. Particulate phosphate concentrations.

daily input coincides with periods of peak river flow. During 1966 and 1967 when inorganic phosphate levels were somewhat depressed, nitrate concentrations were reduced to near zero, indicating that nitrate was in fact limiting the growth of phytoplankton prior to 1969 (Figure 8). On the other hand, during the period 1971-74, nitrate was never reduced to zero during the year, whereas inorganic phosphate frequently could not be detected during the same period. Kootenay Lake probably became phosphate limited in terms of primary production (Chu[24], Goldberg et al.[25], Fogg[26], Lackey[27], Thomas[28]). One should also look to ammonium concentrations (Figure 9) since algal cells may take up ammonium preferentially over nitrate for at least some species (Eppley[29]). An examination of the data shows that in 1967 ammonium levels reached zero at times when nitrate was still present. During 1968, nitrate never reached low levels whereas ammonium frequently was depressed. The same can be said for 1969. During 1971-74 ammonium was reduced during the summer months but was always measurable.

BIOLOGICAL POPULATIONS

Phytoplankton

Chlorophyll a readings have been converted to milligrams per liter dry weight of algae assuming a one-half % concentration of chlorophyll based on series of measurements made during the month of May. This proportion undoubtedly does not remain constant throughout the year, however conversion to dry weight facilitates comparison with similar quantities for zooplankton. There has been a reduction in the number of major phytoplankton peaks since 1969 (Figure 10), but the annual means have decreased only about 10%. Figures for 1971 and 1972 suggest that the phytoplankton levels remain reasonably high throughout the summer, although in 1973 there were distinct peaks in the spring and late summer at all stations. Since there was no distinct period of peak flow or abnormal temperature patterns in 1973, one must look to nutrients and zooplankton for the cause. Here phosphate was essentially zero in midsummer (between peaks), and ammonium levels remained low. Nitrate, on the other hand, seemed to mirror the phytoplankton peaks. This observation suggests that the phytoplankton species present had taken up most of the ammonium and were required to rely on nitrate as a prime source of nitrogen for growth. Since the nitrate levels did not in fact go to zero, one is forced to conclude that phosphate ultimately limited the growth and that perhaps temperature changes the uptake kinetics in such a way that two peaks were produced. One cannot avoid considering a further possibility, that is, grazing pressure brought about by a massive increase in the cladoceran population.

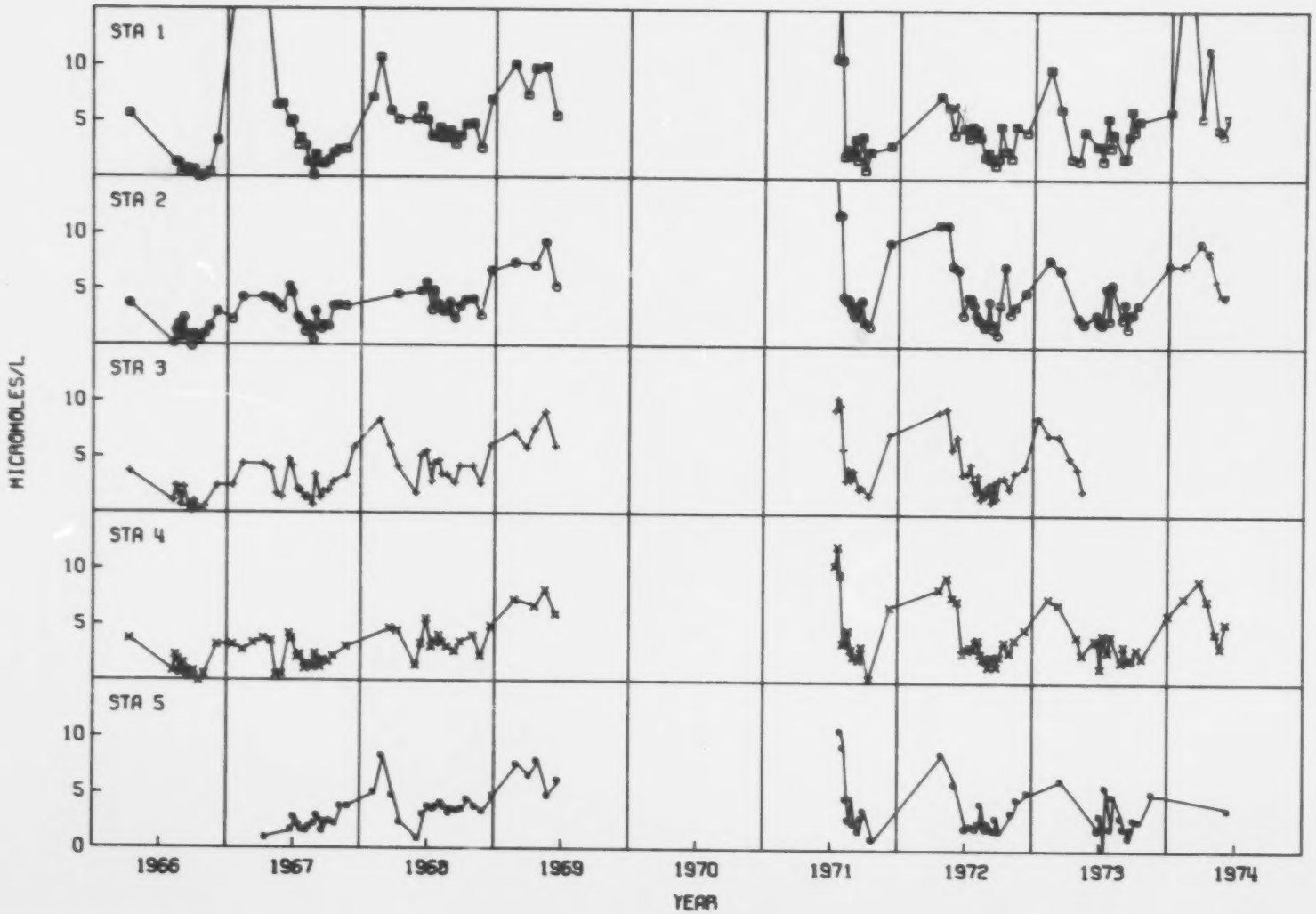

Figure 8. Nitrate concentrations.

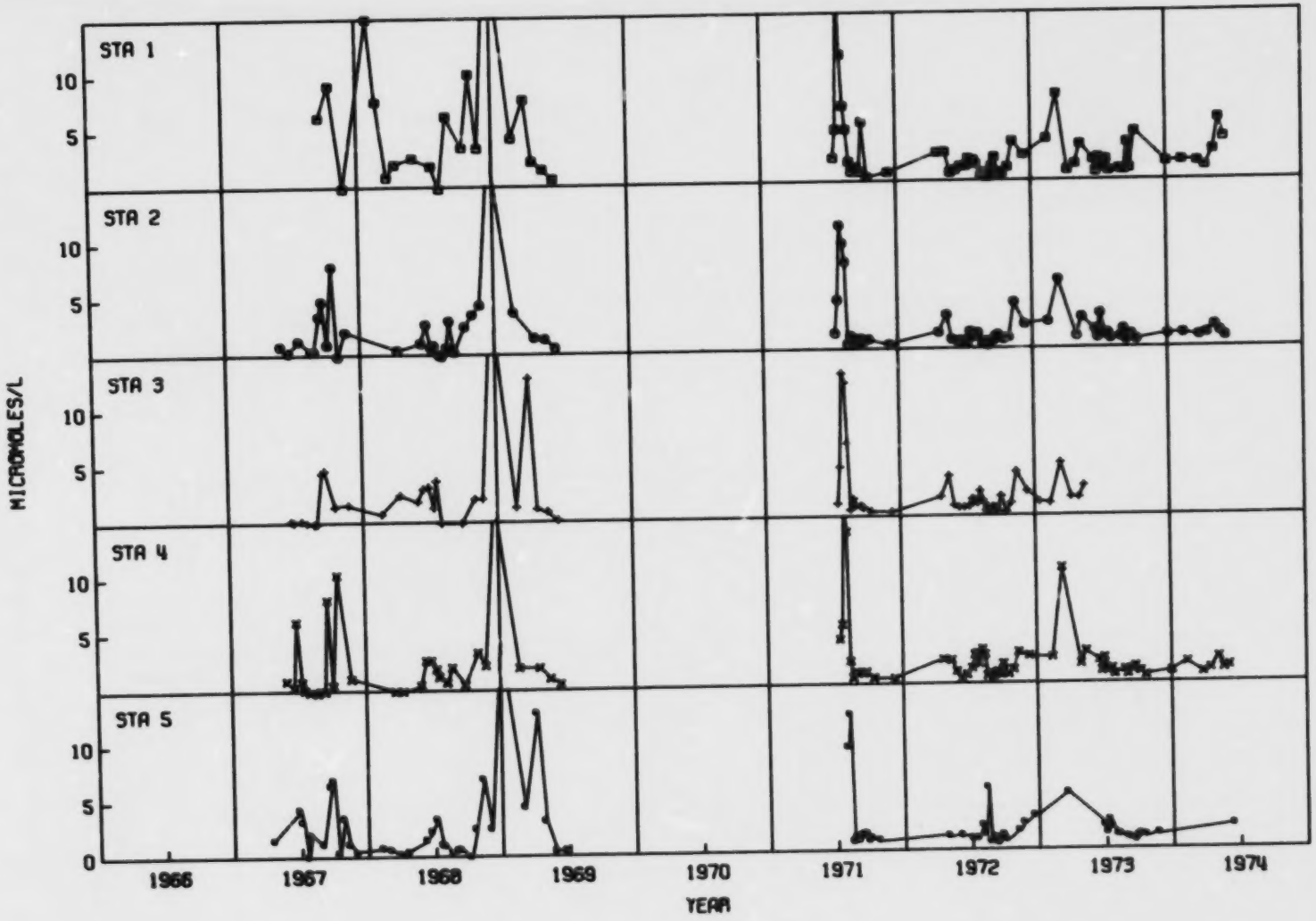

Figure 9. Ammonium concentrations.

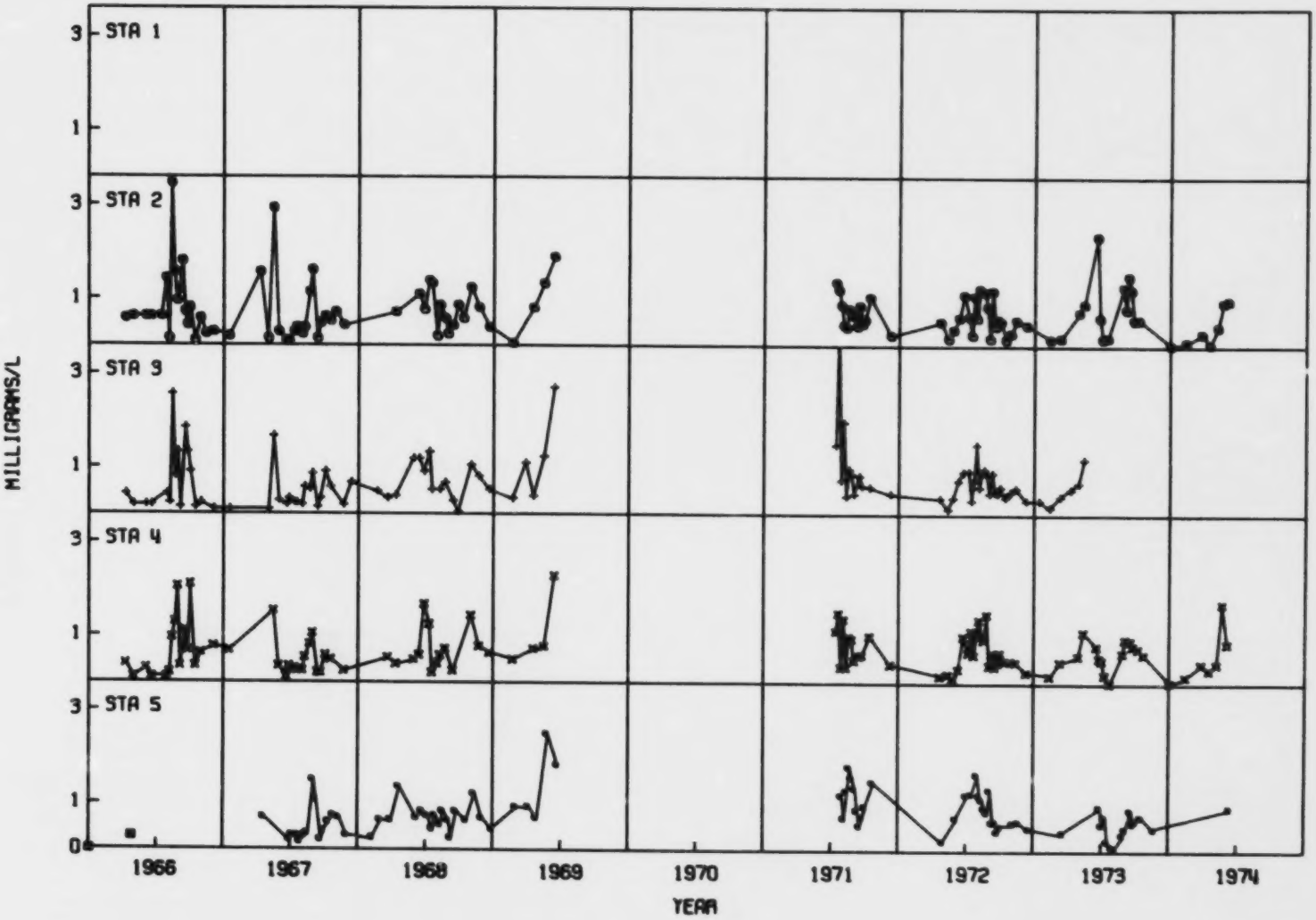

Figure 10. Phytoplankton levels.

Little detail is available on algal composition in Kootenay Lake. During 1965-66, D. Fillion made extensive collections at the lake; however, he did not identify many of the species present in his samples. Subsequent work by G. Ennis, also from the University of British Columbia (unpublished), yielded a list of species present in the lake at that time. This effort was followed in 1973-75 by the unpublished results of Cloern and Prescott. Since the material collected in 1965-66 was not examined by Cloern and Prescott, nor was the material collected by Cloern examined by those reviewing the 1965-66 samples, only generic comparisons seem warranted (Table 2). Unfortunately, specific population densities are not available for further comparison. Lately, among the larger forms, Asterionella is dominant during May and June, followed by Anabaena, Phormidium, and Fragilaria during July, August, and September. Of those genera important in the diet of zooplankton, Cyclotella and Cryptomonas are prevalent from May through August. Of significance here is the fact the Anabaena did not reach bloom proportions in 1973-75, as it did traditionally each August during 66-69. It should also be pointed out that Oscillatoria was not identified for 1973-75, as it had been for 1965-66. Furthermore Stephanodiscus did not appear in 1973-75 as it had earlier. Considerable care must be taken in evaluating the generic lists for the two periods, since the outflow of Duck Lake at the south end of Kootenay Lake empties into the Kootenay River and contributes algal species that may not be typical open water forms. For example, Chlamydomonas, Eudorina, Pandorina, and Volvox were identified in Kootenay Lake, but should not be considered typical of the Kootenay Lake plankton.

Zooplankton

The observed copepod and cladoceran quantities in milligrams per liter were calculated by multiplying numerical densities by 2.5 and 3.5 micrograms per individual, respectively. As with chlorophyll, these values do not remain constant, particularly during periods of peak reproductive activity. The total copepod population tended to peak during late summer and early fall, although they were represented in the lake throughout the year (Figure 11). The cladocerans, too, peaked in late summer; however, they were virtually absent from the lake during the balance of the year (Figure 12).

Table 2. Algal genera identified from Kootenay Lake for 1965-66 by Fillion *et al* (unpublished) and for 1973-75 by Cloern and Prescott (unpublished)

	1965-66	1973-75
Cyanophyta		
Anabaena	X	X
Microcystis		X
Merismopedia		X
Oscillatoria	X	
Phormidium		X
Cryptophyta		
Chroomonas	X	X
Cryptomonas	X	X
Pyrrophyta		
Ceratium	X	X
Gymnodinium	X	X
Peridinium		X
Peridiniopsis	X	
Chrysophyta		
Dinobryon	X	
Mallomonas	X	X
Chlorophyta		
Ankistrodesmus	X	X
Botryococcus		X
Chlamydomonas	X	
Cladophora	X	
Cosmarium	X	
Crucigenia	X	
Dictyosphaerium		X
Dispora	X	
Elakatothrix	X	
Eudorina		X
Gemellicystis	X	
Kirchneriella	X	
Lagerheimia	X	
Oocystis		X
Pandorina	X	X
Scenedesmus	X	X
Staurastrum		X
Tetraedron		X
Trepomonas	X	
Ulothrix	X	
Volvox		X
Bacillariophyta		
Achnanthes	X	
Asterionella	X	X
Caloneis	X	
Cocconeis	X	X
Cyclotella	X	X
Cymbella	X	X
Diatoma	X	X
Epithemia	X	X
Fragillaria	X	X
Gomphonema	X	X
Hannaea	X	
Melosira	X	X
Meridion		X
Navicula	X	X
Nitzschia	X	
Opephora	X	
Rhizosolenia	X	
Stephanodiscus	X	
Synedra	X	X
Tabellaria	X	X

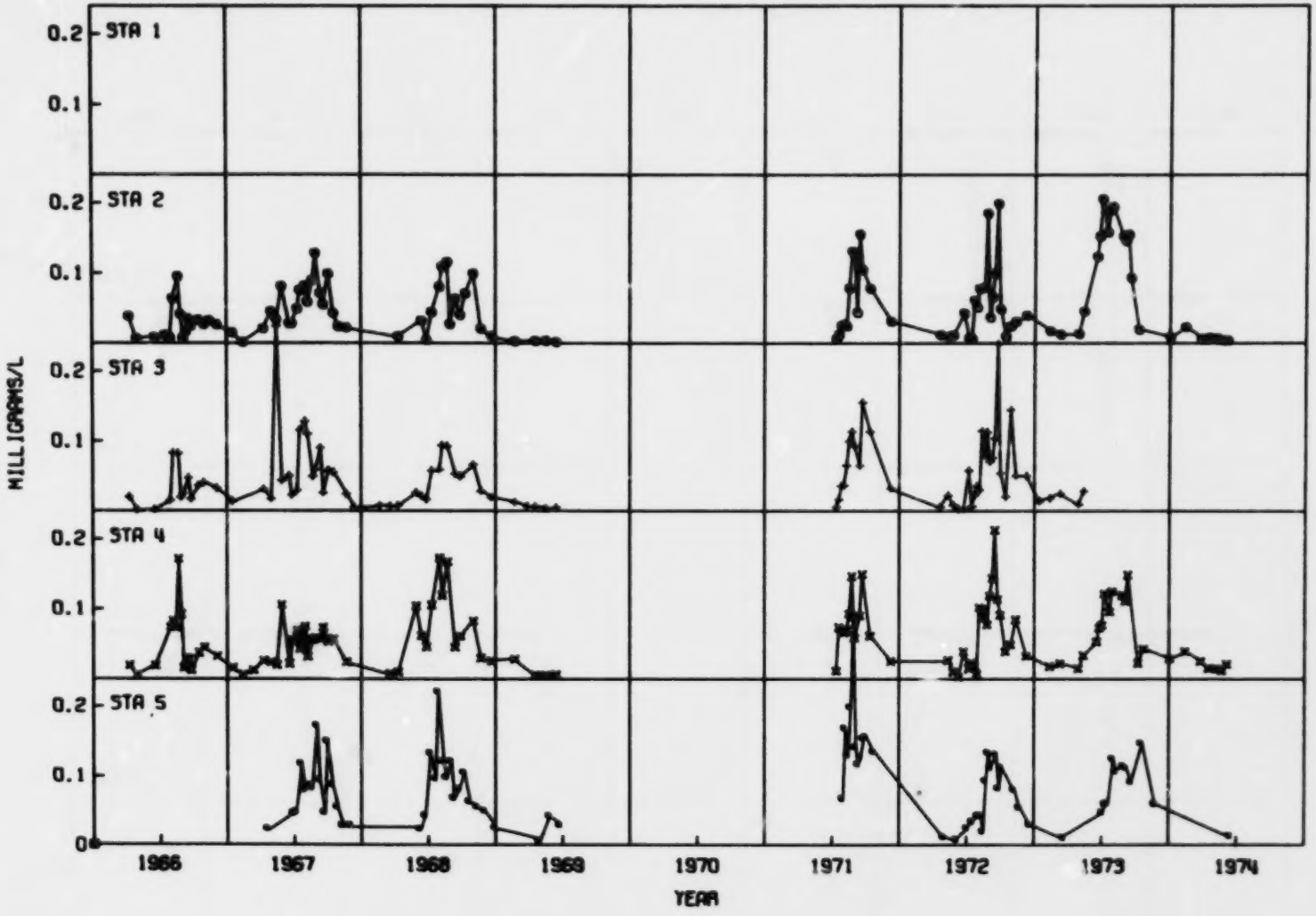

Figure 11. Copepod levels.

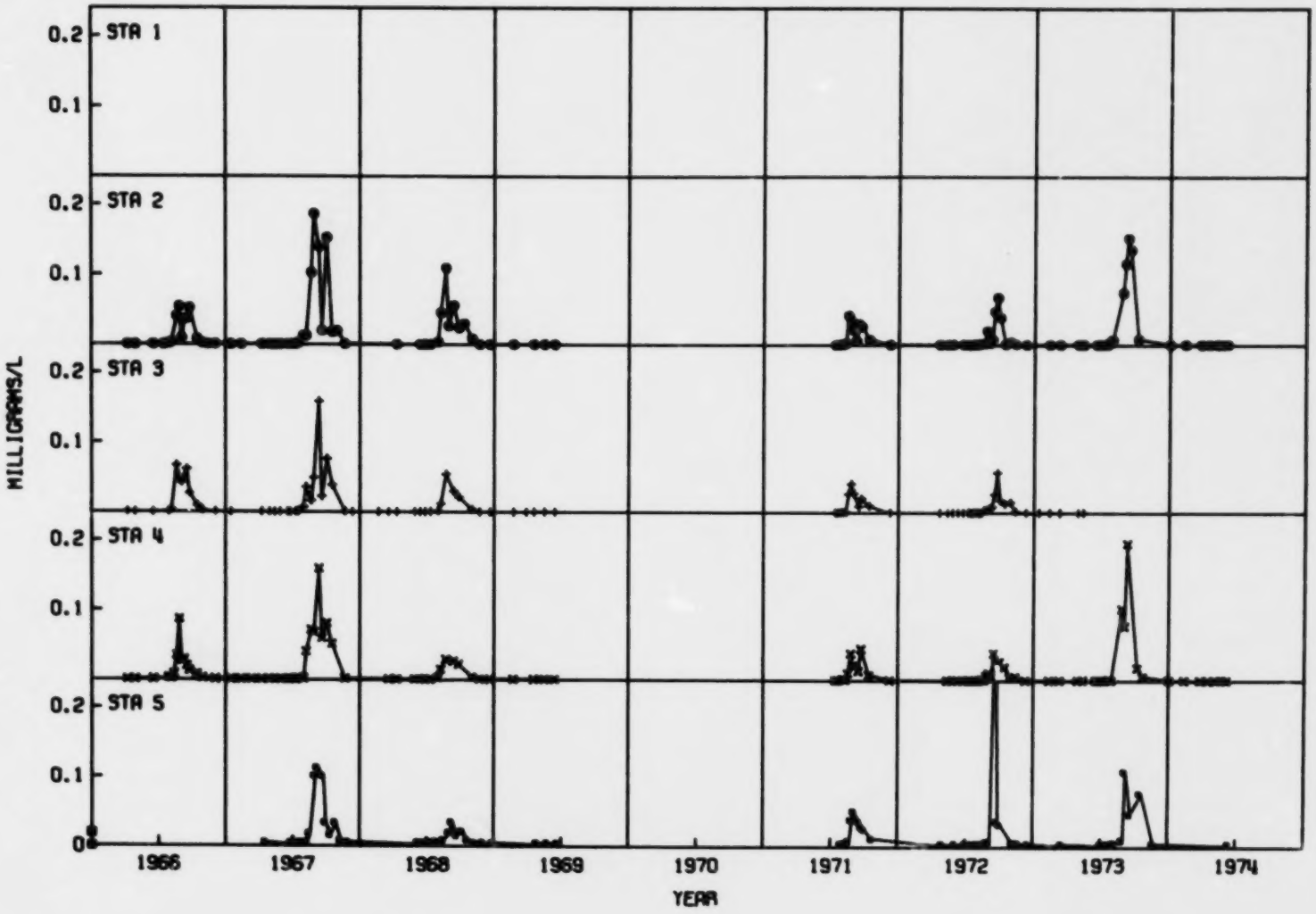

Figure 12. Cladoceran levels.

Two copepods are common in Kootenay Lake, Cyclops bicuspidatus, and Diaptomus ashlandi, and three cladocerans, Daphnia galeata, Diaphanosoma leuchtenbergianum, and Bosmina coregoni. A detailed evaluation of the seasonal reproductive activity of each of these five species was made. Figure 13 presents the total densities of each species at Station 2. This is followed in Figure 14 by a summary of those cladocerans with eggs and copepods with egg sacks. Note that during 1966-69, Diaptomus reached essentially the same level each summer. Cyclops on the other hand appeared to be increasing during the three-summer study. The years 1971-73 saw increasing summer peaks of Diaptomus as well as Cyclops. Daphnia reached substantial densities during 1967, but was relatively low during 1966 and 1968. This genus has continued to decline and during 1971-74 was essentially absent from the lake. Diaphanosoma, in contrast, has increased markedly during 1971-73, reaching levels second only to Diaptomus. Bosmina never has contributed substantially to the total zooplankton population, but recently it has been as abundant as Daphnia. These changes could be induced by selective predation by landlocked sockeye salmon (Brooks and Dodson[30], Brooks[31], Galbraith[32], Warshaw[33], Wells[34]) or by competition among zooplankters (Hall et al.[35], Hazelwood and Parker[36]).

Although the total copepod density did not vary considerably from summer to summer during 1966-68, a larger number of individuals were gravid during 1967 than during the other two years. Furthermore, even though 1972 was a year of high Diaptomus populations, only a relatively small proportion of the population was carrying egg sacks. Cladocerans also, as exemplified by Diaphanosoma, exhibited a rather erratic relationship between the size of the population and the number of gravid members in it. This may be due to differences in number of young per brood. Other possibilities include lower mid-summer natural mortality rates as well as lower grazing pressure. Information comparable to that given for Station 2 in Figures 13 and 14 is given in Figures 15 and 16 for Station 3, Figures 17 and 18 for Station 4, and in Figures 19 and 20 for Station 5. Recall that Station 5 is located slightly north of the point where water leaves the lake via the west arm. Cladoceran populations are remarkably similar at all four Stations, although the copepod populations at Station 5 do not appear to follow the same pattern as those at Stations 2-4 during 1971-74. Noteworthy is the fact that the population of Diaptomus was approximately twice as high in 1973 at Stations 2-4 than at Station 5.

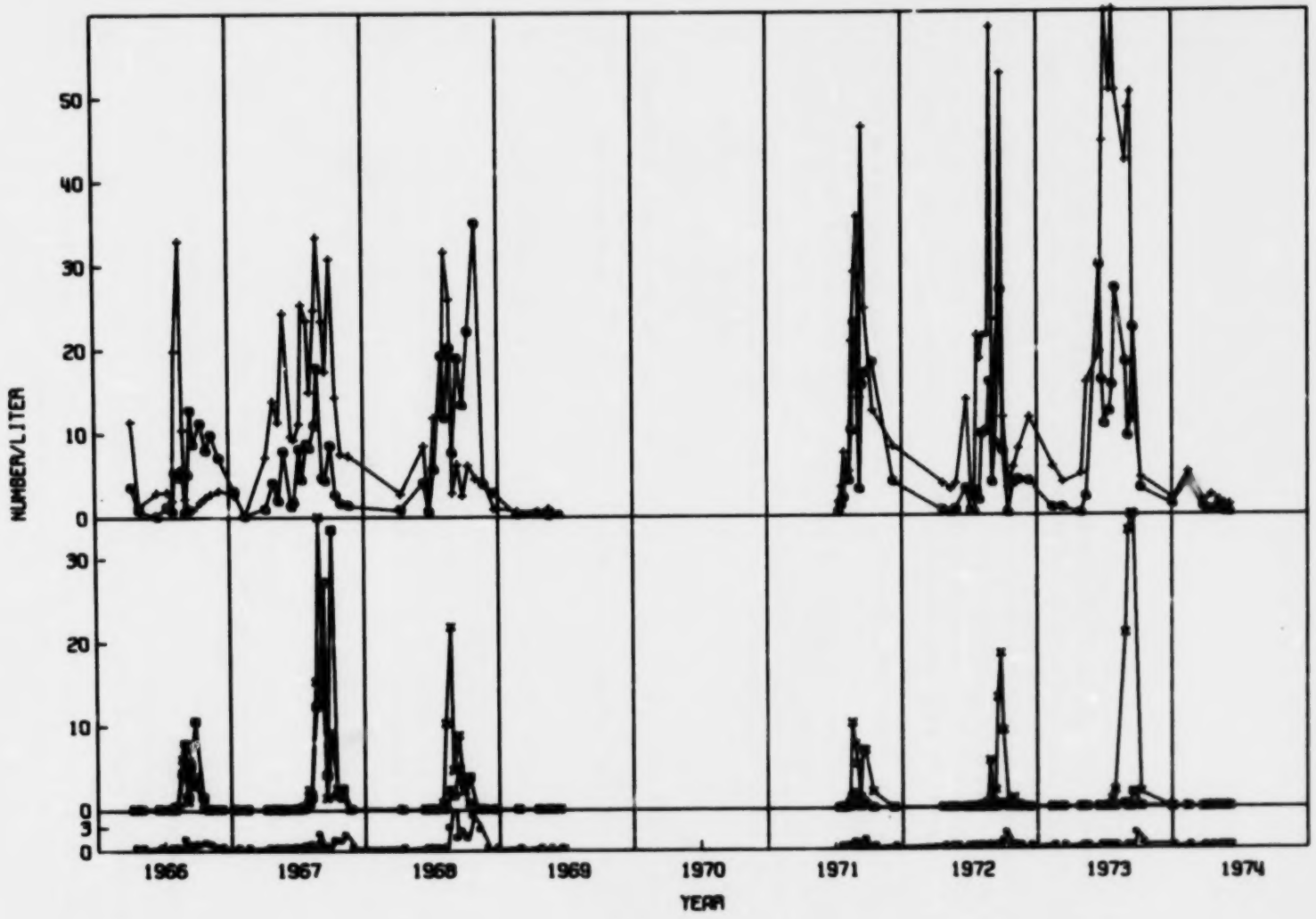

Figure 13. Total zooplankton densities at Station 2.

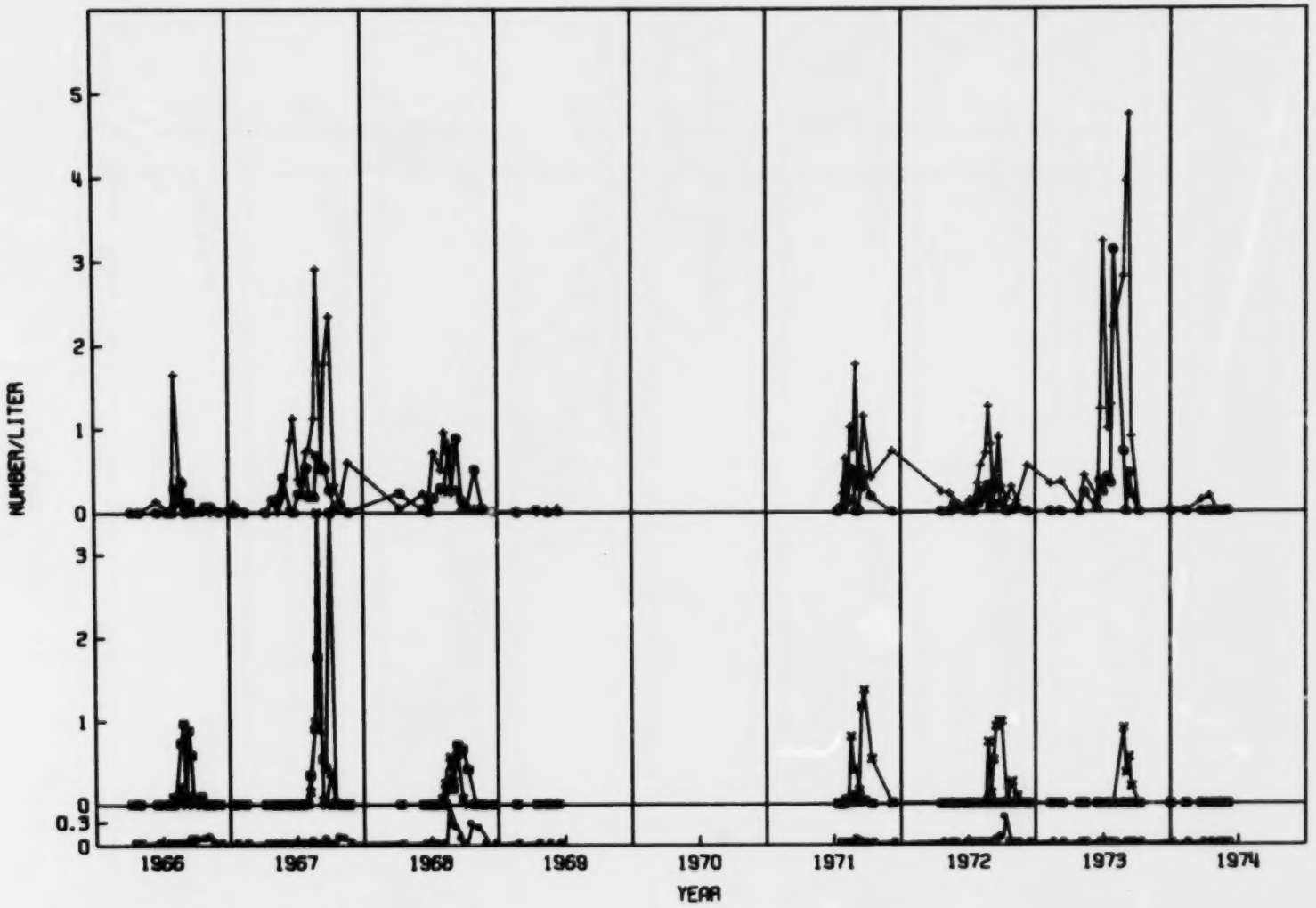

Figure 14. Gravid zooplankton densities at Station 2.

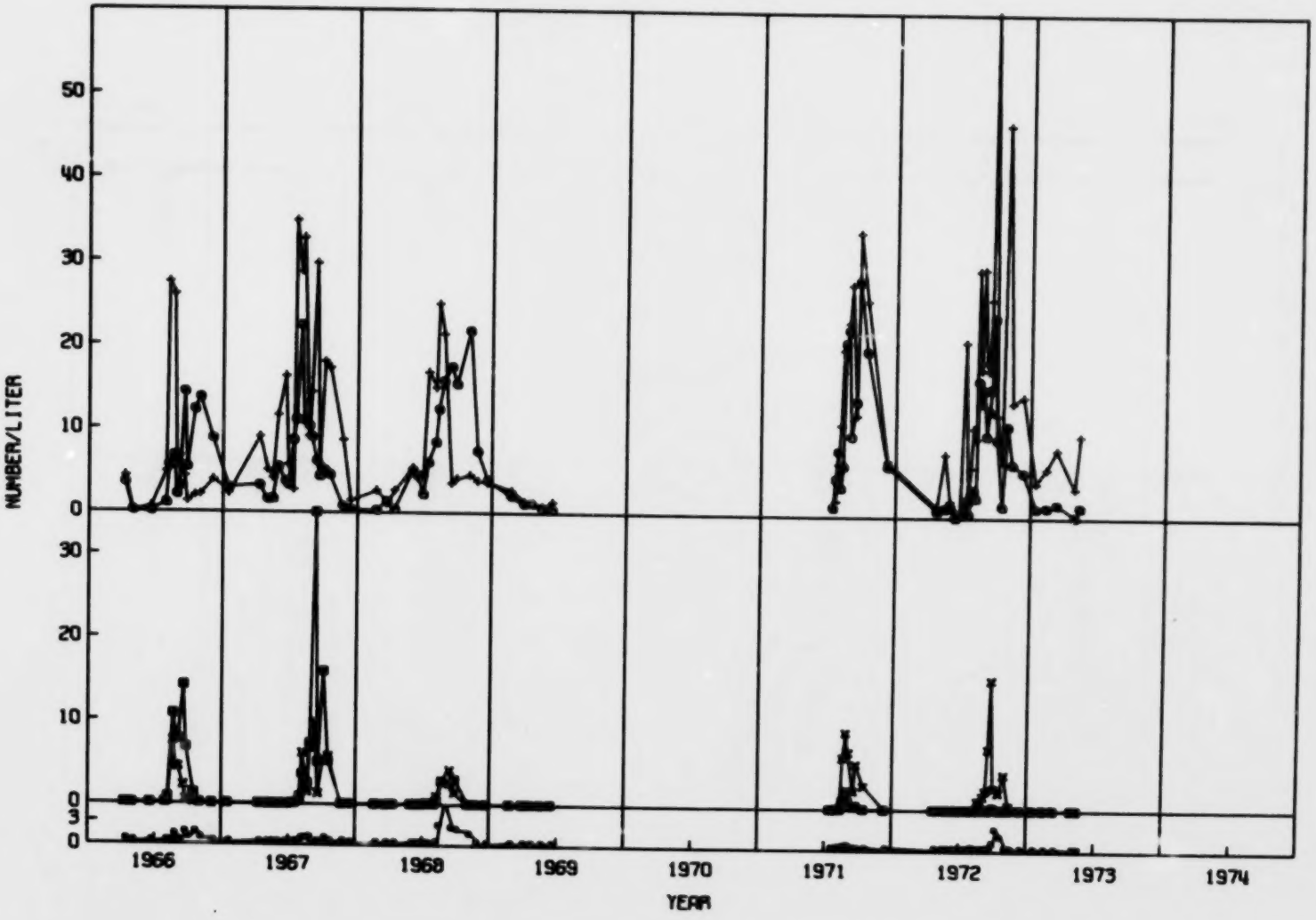

Figure 15. Total zooplankton densities at Station 3.

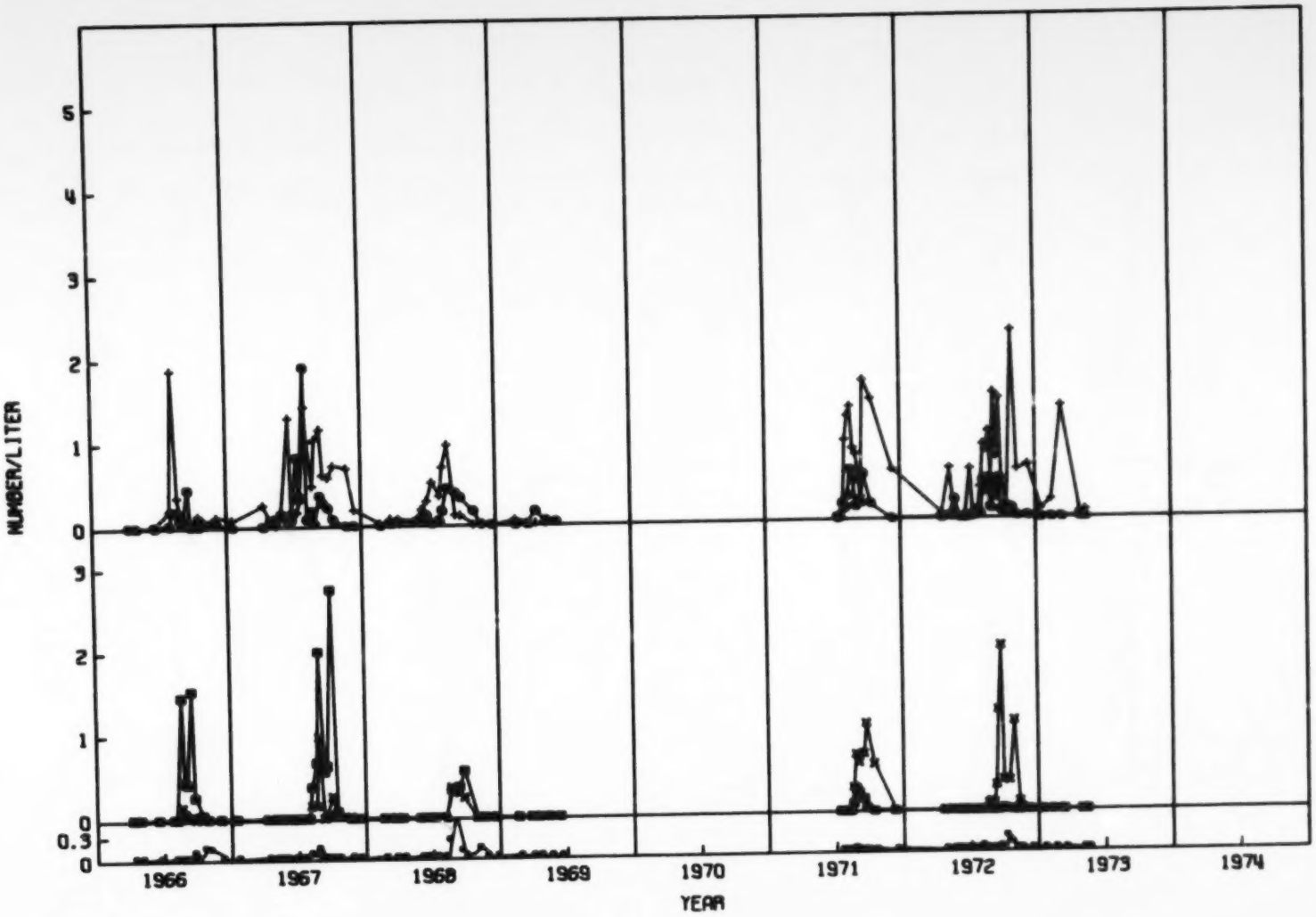

Figure 16. Gravid zooplankton densities at Station 3.

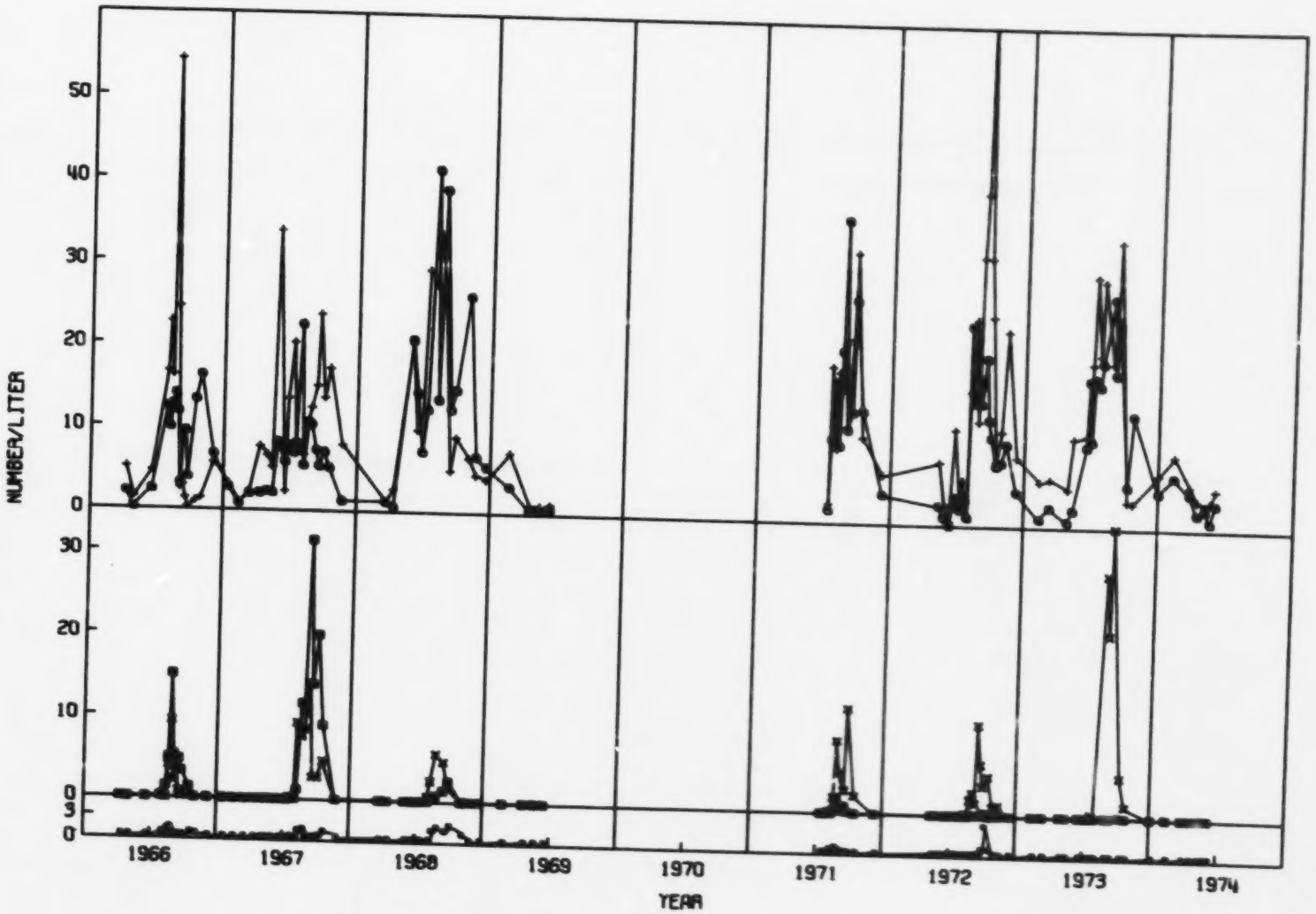

Figure 17. Total zooplankton densities at Station 4.

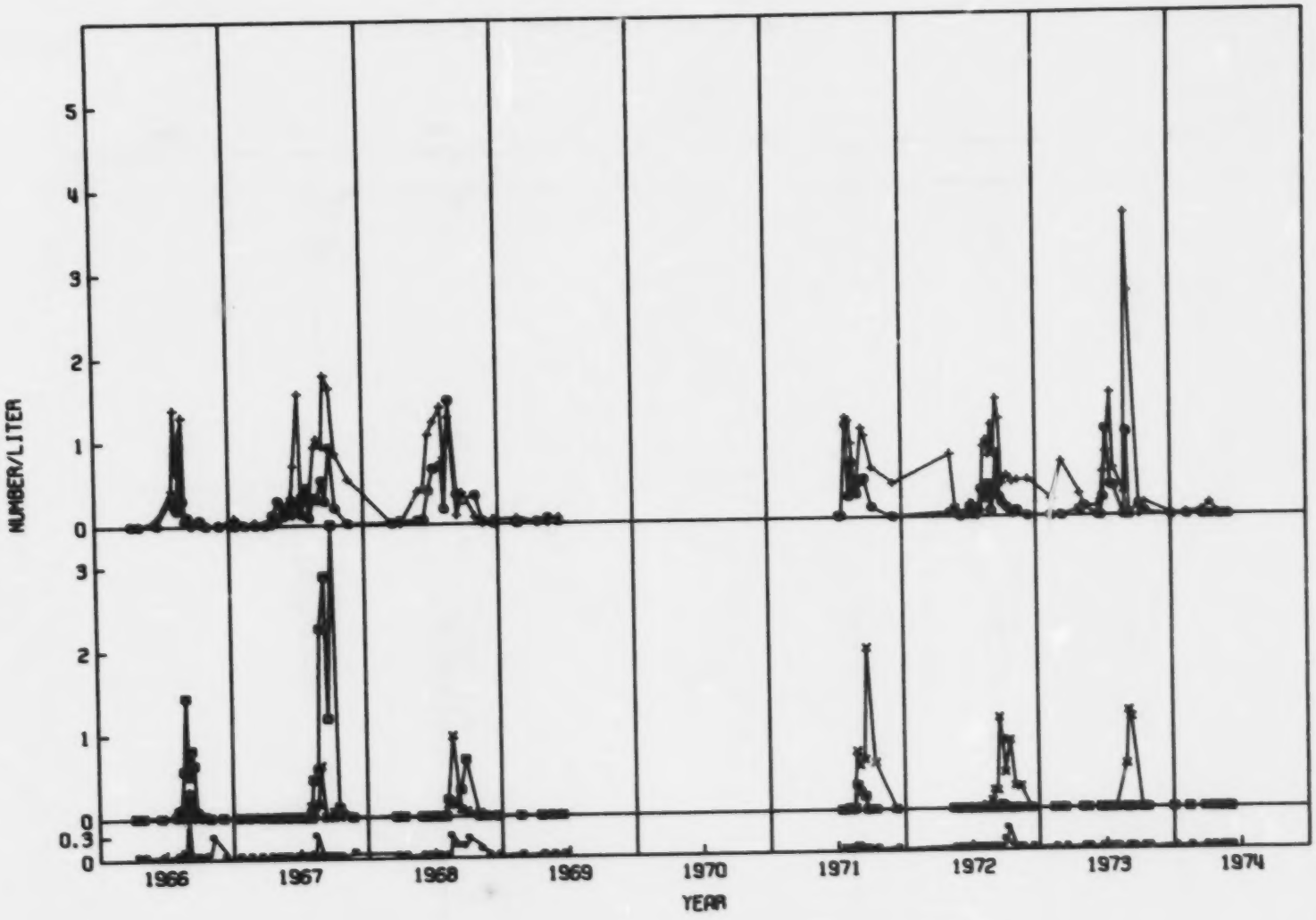

Figure 18. Gravid zooplankton densities at Station 4.

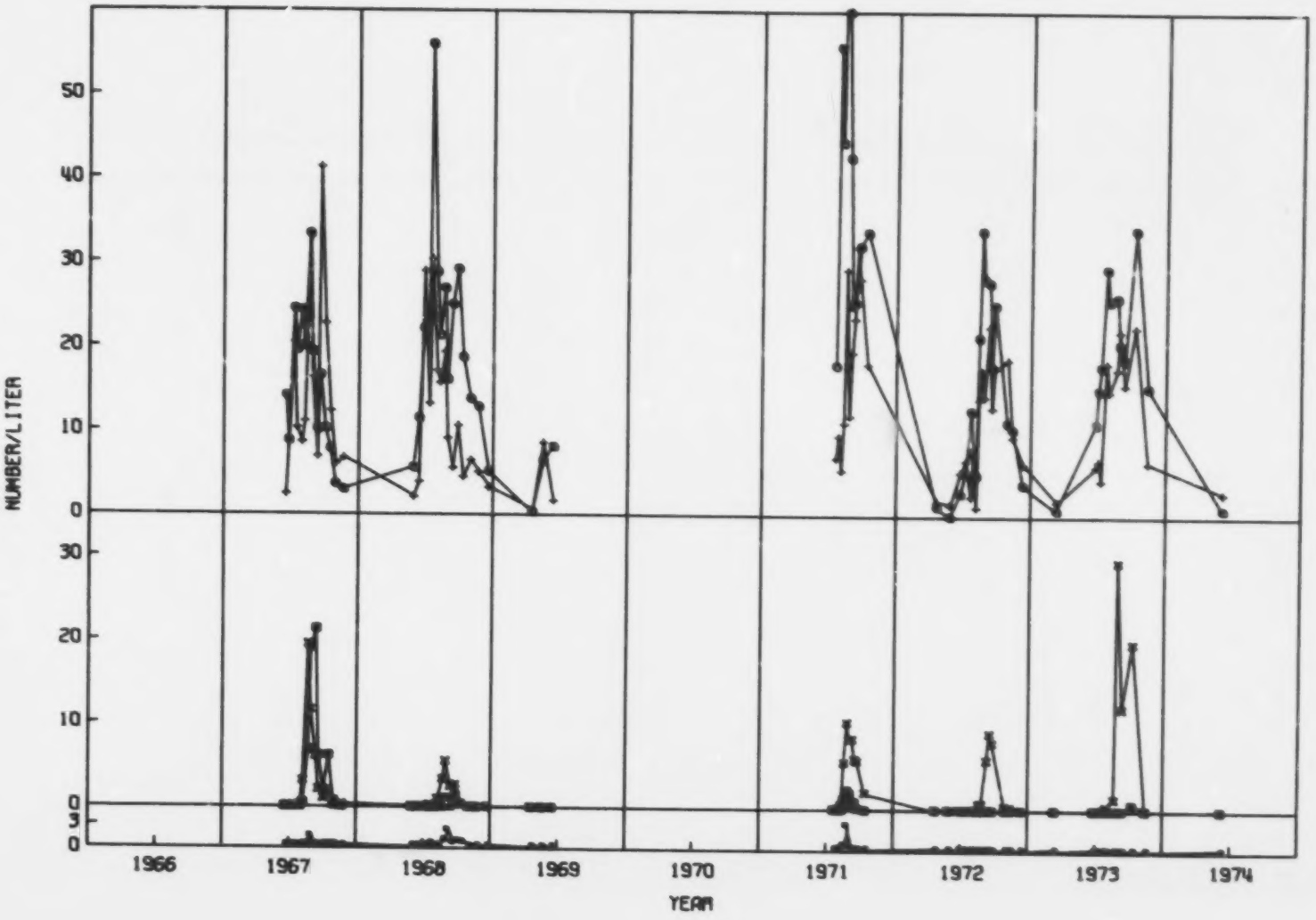

Figure 19. Total zooplankton densities at Station 5.

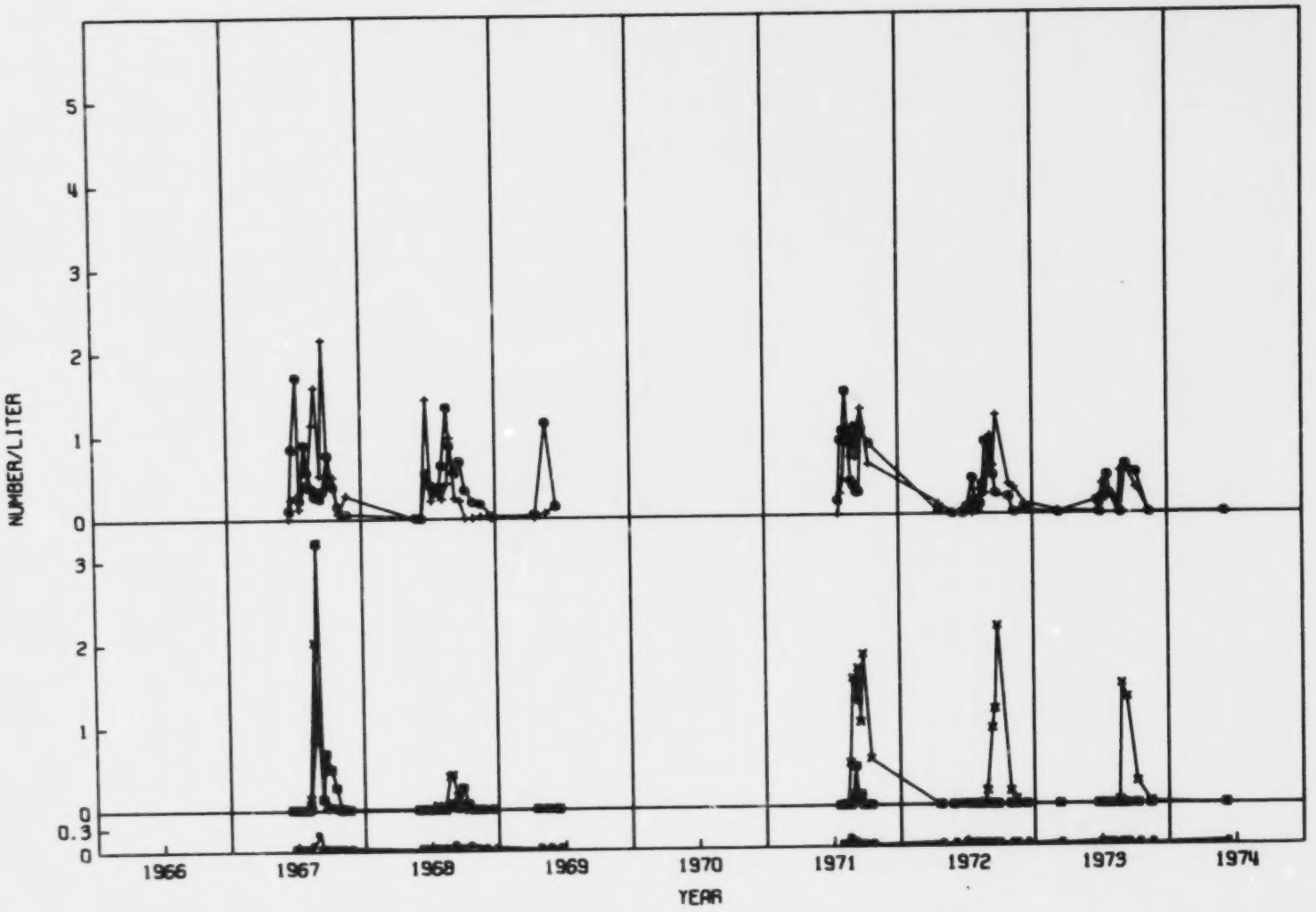

Figure 20. Gravid zooplankton densities at Station 5.

SECTION V

SIMULATION MODEL

PARAMETER ESTIMATION

All models of ecological systems contain various rate and proportionality constants, as well as other coefficients, that must be given specific values before simulated results can be generated. Many of these parameters may be estimated from field or laboratory observations, and others taken from similar situations reported in the literature. Unfortunately some quantities cannot be measured, although they exist and are conceptually important in model development. In these cases, it becomes desirable to obtain estimates by fitting part or all of the model to data gathered from the system under study. The general procedure follows.

Suppose the model system is described by the set of differential equations

$$y_i' = f_i(\underline{y}, \underline{p}) \qquad , i = 1,\ldots,n \tag{2}$$

where y_i' is the time derivative of the i^{th} state variable y, an element of the vector $\underline{y}$, and $\underline{p}$ is a vector of parameters. For fixed $\underline{p}$, the system may be viewed as consisting of ordinary differential equations. If, on the other hand, $\underline{p}$ is allowed to vary, y_i' is more appropriately viewed as the partial differential equation

$$\frac{\partial y_i}{\partial t} = f_i(\underline{y}, \underline{p}). \tag{3}$$

The effect of changing p_j $(j = 1,\ldots,m)$ on the solution y_i of this equation is found by first writing

$$\partial\left(\frac{\partial y_i}{\partial t}\right)/\partial p_j = \sum_{k=1}^{m} (\partial f_i/\partial y_k)(\partial y_k/\partial p_j) + \partial f_i/\partial p_j. \tag{4}$$

But the order of differentiation can be reversed yielding

$$\partial\left(\frac{\partial y_i}{\partial p_j}\right)/\partial t = \sum_{k=1}^{m} (\partial f_i/\partial y_k)(\partial y_k/\partial p_j) + \partial f_i/\partial p_j. \tag{5}$$

Now let $\partial y_k/\partial p_j$, the sensitivity of y_k to p_j, be designated as u_{kj} and rewrite as

$$\partial u_{ij}/\partial t = \sum_{k=1}^{m} (\partial f_i/\partial y_k)\, u_{kj} + \partial f_i/\partial p_j. \tag{6}$$

Taken over all i and j, this produces a system of linear differential equations in u that can be solved in concert with the original system describing state variable behavior through time.

With this background the approach used to estimate $\underline{p}$ proceeds along the following lines. Suppose $\underline{\hat{y}}$ are the observed values of $\underline{y}$ at sampling time T. Suppose further, that an objective function of the form

$$D = \sum_{Ti}\sum (\hat{y}_i - y_i)^2 \quad , \tag{7}$$

$$D = \sum_{Ti}\sum (\hat{y}_i - y_i)^2/y_i \quad , \tag{8}$$

or

$$D = \sum_{Ti}\sum [(\hat{y}_i - y_i)/y_i]^2 \tag{9}$$

is selected for minimization (others could be justified including the use of $\hat{y}_i$ in the denominator to reduce computation). Now differentiate D with respect to p_j, D_j say, and expand in a Taylor Series around initial approximations $\tilde{\underline{p}} = \hat{\underline{p}} - \underline{\Delta p}$ ($\hat{\underline{p}}$ a solution) to give

$$D_j(\tilde{\underline{p}} + \underline{\Delta p}) \simeq \sum_k \Delta p_j (\partial D_k/\partial p_j)\Big|_{p_j = \tilde{p}_j} = 0. \tag{10}$$

The resulting system is linear in, and can be solved repeatedly for $\underline{\Delta p}$ to update $\underline{p}$. This approach should be recognized as Newton's method. Still other techniques can be applied including conjugate gradients and steepest descent (see, e.g., Powell[37]).

Now observe, for example, that

$$D_j = \partial D/\partial p_j \tag{11}$$

$$= -2\sum_{Ti}\sum (\hat{y}_i - y_i)u_{ij} \quad ,$$

$$\text{and } D_j(\tilde{\underline{p}} + \underline{\Delta p}) \simeq \sum_{kTi}\sum\sum \Delta p_k[(\hat{y}_i - y_i)\partial u_{kj}/\partial p_j - u_{kj}^2] = 0. \tag{12}$$

Here one is required to compute values of the second derivatives of y_i with respect to all p_j, that is, a massive system of n state variable equations (differential) plus nm sensitivity equations plus nm^2 second derivative equations must be solved at every T, usually numerically. The last set of nm^2 equations can be avoided by expanding y_i about $\underline{p}$ in D and finding the derivative of D with respect to Δp_j (D'_j say):

$$D = \sum_{Ti}\sum(\vartheta_i - \sum_k \Delta p_k u_{kj})^2 \qquad (13)$$

and $$D'_j(\bar{p} + \Delta p) = \sum_{LTi}\sum\sum(\vartheta_i - \sum_k \Delta p_k u_{kj})u_{Lj} = 0,\ L = 1,\ldots,m. \qquad (14)$$

To avoid inverting ill-conditioned matrices, the p_j should be scaled so that all parameters are of the same order of magnitude. Furthermore, if the magnitudes of the state variables are not of the same order, care must be taken to scale the n components of the objective function D.

VARIABLES INCLUDED

Parker[38,39,1,2] has attempted to create a reliable series of predictive models that relate the state and driving variables in Kootenay Lake. The variables used in the most recent version of the model (Parker[1]) are given in Table 3.

Table 3. VARIABLES USED IN THE NUTRIENT PLANKTON MODEL OF THE MIXED LAYER IN KOOTENAY LAKE

Driving Variables	State Variables
Inputs	Summer algal assemblage (group 1)
Volume flow	Spring algal assemblage (group 2)
Inorganic phosphate	Inorganic phosphate
Nitrate	Nitrate
Ammonium	Ammonium
	Copepods
Temperature	Cladocerans
Solar Radiation	
Transparency	

GROWTH AND DEATH RATES

Dynamic models based on differential equations require mathematical descriptions of growth and death processes in terms related to the driving variables. The growth rate of the two algal groups

considered (spring and summer assemblages) were made functions of solar radiation, temperature, and the three nutrients: phosphate, nitrate, and ammonium. In addition, mortality rates due to natural causes and predation were also functions of temperature. Cladoceran and copepod growth rate was largely a function of grazing activity and temperature, mortality rates largely attributed to temperature. Specific functions selected to relate algal growth to light intensity and temperature are discussed in Parker[1,4]. Monod relationships were used to describe dependence on the nutrients, with pooled nitrogen used as a single variable. All of the underlying relationships used to describe growth and mortality rates are given in Table 4. In addition, the differential equations used to describe the seven state variables in the system are tabulated. Note that horizontal transport due to incoming Kootenay River water, as well as vertical transfer, have been incorporated in these equations. Essentially, the differential equations for the three nutrients are mass balance forms which assume that all of the nutrients ingested but not incorporated into new zooplankton are immediately recycled. Also any nitrate that has been reduced and used by phytoplankton for growth will be returned to the system as ammonium. Specific values used for all of the constants shown in Table 4 are summarized in Table 5.

COMPARISON WITH OBSERVED VALUES

The model outlined in Table 4 was developed primarily from information gathered during the period 1966-69 while phosphate input was high. The primary objective of the modeling effort was to predict the consequences of reduced phosphate input. Once the model was completed and "tuned" to 1966-69 data (Parker [1,39]), it was applied using input data from 1971-74. Only one constant was changed in Table 5 for this application. For use over 1966-69, the half-saturation constant for phosphate was 1.0 for both algal groups. This is, of course, a very high figure, its use being consistent only with very high ambient phosphate levels prior to 1969. It was assumed that phytoplankton in the system would slowly adjust to the new phosphate levels by gradually reducing the half-saturation constant to a more typical value. A review of model behavior under different assumptions of reduced half-saturation constant suggested as appropriate a linear decrease from 1.0 in 1971 to 0.2 in 1974. Failure to reduce the half-saturation constant resulted in the virtual loss of the phytoplankton populations in 1973 and 1974.

Simulated values for inorganic phosphate, nitrate, and ammonium are presented in Figures 21, 22, 23, respectively. These figures should be compared to Figures 5, 8, and 9, respectively.

Table 4. THE MODEL SYSTEM

	Growth rate (G)	Mortality rates	
		Natural (M_1)	Predation (M_2)
Algal group 1 (A_1)	$a_{11}e_1(I)f_1(T)g_1(N_1)h_1(N_2,N_3)$	$a_{21}T$	$TB(c_{11}C_1+c_{21}C_2)$
Algal group 2 (A_2)	$a_{21}e(I)f_2(T)g_2(N_1)h_2(N_2,N_3)$	$a_{22}T$	$TB(c_{12}C_1+c_{22}C_2)$
Cladocera (C_1)	$b_1TB(c_{11}A_1+c_{12}A_2)$	$c_{13}T$	$c_{14}TC_1$
Copepoda (C_2)	$b_2TB(c_{21}A_1+c_{11}A_2)$	$c_{23}T$	$c_{24}TC_2$

I = light intensity
T = temperature
N_i = nutrients
$e_1(I) = (I/I_{si})\exp(1-I/I_{si})$

$f_1(T) = [(T/T_{s1})\exp(1-T/T_{si})]^{\alpha_1}$
$g_1(N_1) = N_1/(K_{11} + N_1)$
$h(N_2,N_3) = (N_2+N_3)/(K_{21}+N_2+N_3)$
$B = \exp[-k(A_1+A_2)]$

Differential equations

$$A_1' = A_1(G_{A1} - M_{1A1} - M_{2A1}) - V\partial A_1/\partial Y$$

$$A_2' = A_2(G_{A2} - M_{1A2} - M_{2A2}) - V\partial A_2/\partial Y$$

$$C_1' = C_1(G_{C1} - M_{1C1} - M_{2C1}) - V\partial C_1/\partial Y$$

$$C_2' = C_2(G_{C1} - M_{1C2} - M_{2C2}) - V\partial C_2/\partial Y$$

$$N_1' = q(A_1M_{2A1} + A_2M_{2A2} - C_1G_{C1} - C_2G_{C2}) - q(A_1G_{A1} + A_2G_{A2}) + m\partial N_1/\partial Z - V\partial N_1/\partial Y$$

$$N_2' = -n_1(A_1G_{A1} + A_2G_{A2})N_2/(N_2 + N_3) + m\partial N_2/\partial Z - V\partial N_2/\partial Y$$

$$N_3' = n_1(A_1M_{2A1} + A_2M_{2A2}) - n_2(C_1G_{C1} + C_2G_{C2}) - n_1(A_1G_{A1} + A_2G_{A2})N_3/(N_2 + N_3) + m\partial N_3/\partial Z - V\partial N_3/\partial Y$$

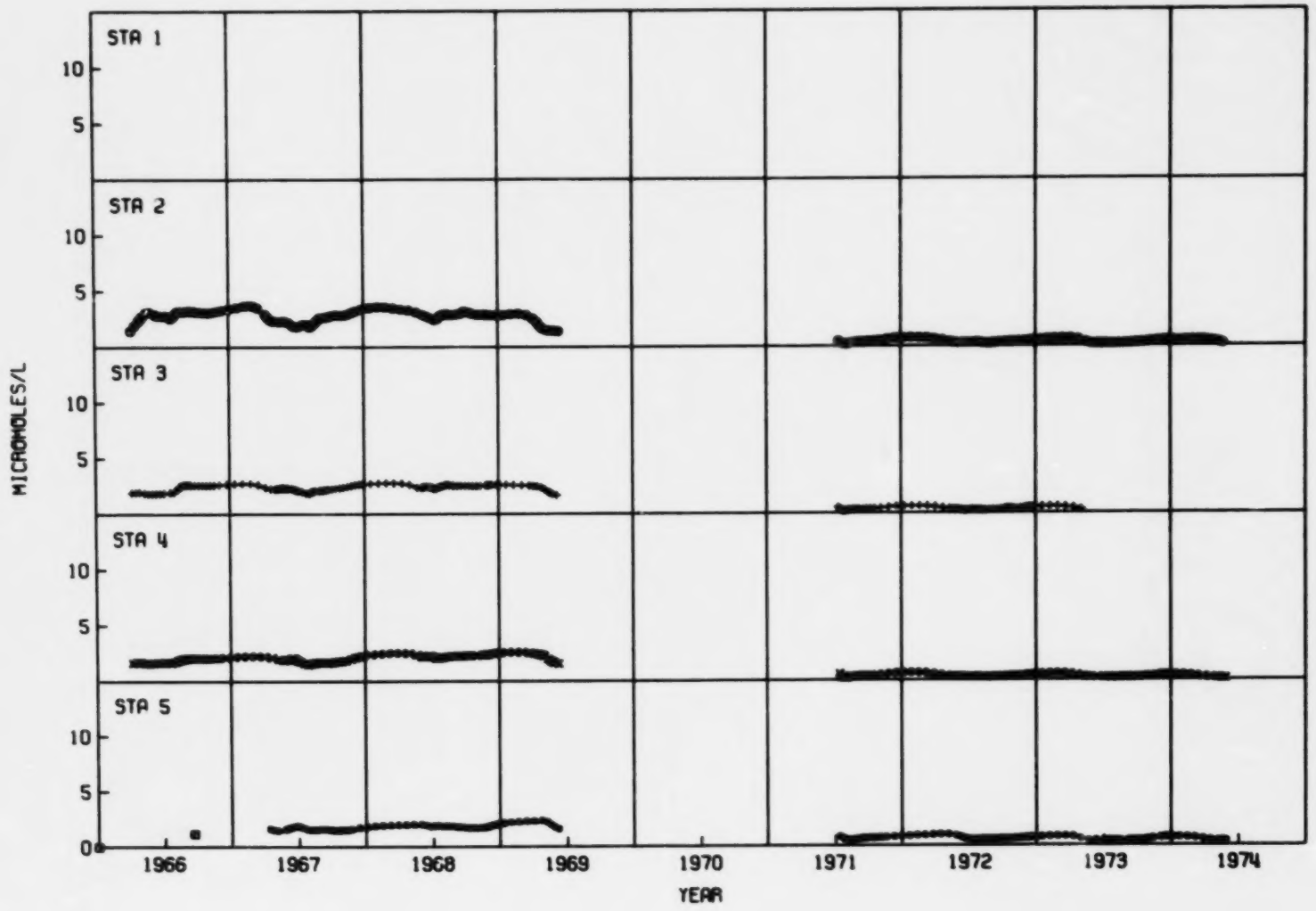

Figure 21. Simulated soluble inorganic phosphate concentrations.

Table 5. CONSTANTS USED IN THE SIMULATION MODEL

$a_{11} = 35.$	$c_{11} = 0.70$	$K_{11} = K_{12} = 1^*$
$a_{12} = 0.02 = a_{21}$	$c_{12} = 0.10$	$K_{21} = K_{22} = 6$
$a_{21} = 8.$	$c_{13} = 0.03$	$q = 0.3$
$I_{S1} = I_{S2} = 1.6$	$c_{14} = 1.5$	$n_1 = 2.0$
$T_{S1} = 20.$	$c_{21} = 0.3$	$n_2 = 5.0$
$T_{S2} = 11.$	$c_{22} = 0.15$	$m = 0.15 \times 10^3$
$\alpha_1 = 4.80$	$c_{23} = 0.015$	
$\alpha_2 = 1.45$	$c_{24} = 0.5$	
	$b_1 = b_2 = 0.47$	
	$k = 0.35$	

*$K_{11} = K_{12}$ decreased linearly from 1 to 0.2 during 1972-74.

The agreement between predicted and observed values for phosphate is reasonably good except during the summers of 1966 and 1967. In 1966 there was an influx of phosphate in the Kootenay River which was not accounted for by the model. Still, there was more spring phytoplankton (group 2) model growth than in the lake.

Nitrogen metabolism in the lake is assessed largely in terms of nitrate and ammonium concentrations. Examination of Figure 22 and the corresponding Figure 8 for observed values indicates that the largest deficiency in model output for the period 1966-69 is that the simulated values are too low at times when the observed nitrate concentrations are high in the lake, resulting in model values being drawn down too low during mid-summer (see for example 1968 and the spring of 1969). During 1971-74 the model is not as responsive as appears necessary to mimic the actual situation in Kootenay Lake. For example predicted winter and spring values for 1972 are low, and the summer values in 1972 and 1973 appear too high. Examination of Figures 23 and 9 shows model

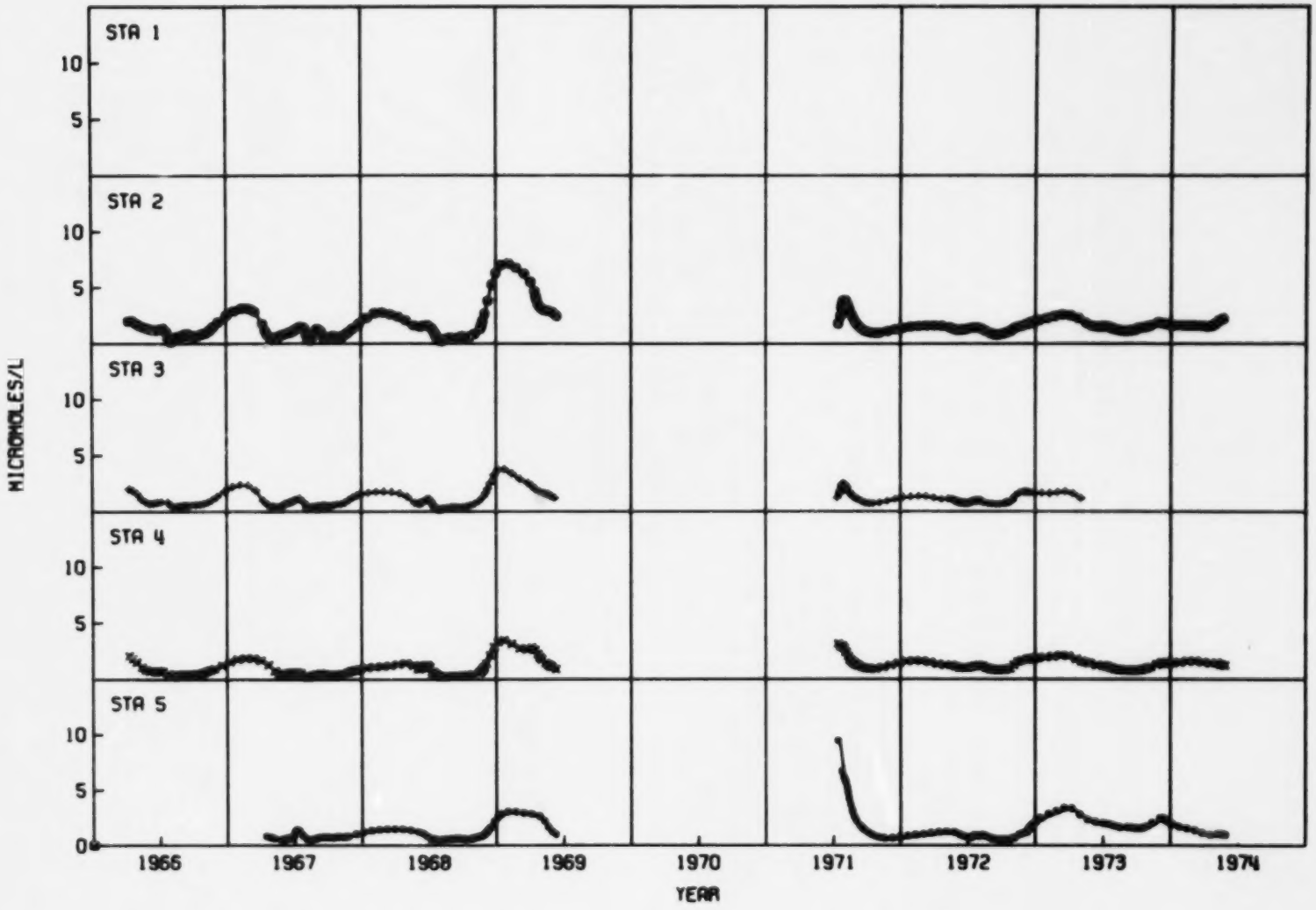

Figure 22. Simulated nitrate concentrations.

values being consistent with observed values during periods of low concentration but substantially too low during periods of high ammonium concentration. This may be due to inadequate contributions by zooplankton during peak periods of growth and contributions from the sediments during the continuous period of winter circulation.

Figure 24 presents the simulated values for the two algal assemblages in Kootenay Lake. Comparison with Figure 10 shows that the largest problem area lies in simulating the late summer algal population. Assuming that the two assemblages provide a reasonable breakdown for phytoplankton in Kootenay Lake, the model algal group 1 rarely ever reaches the levels attained in Kootenay Lake. Apparently nutrient levels in the model are not adequate to produce the required magnitude in late summer.

Simulated copepod densities are given in Figure 25, for comparison with observed values in Figure 11. Although the model values are reasonably good for 1966-1969, they are substantially low for 1971-1974. This is particularly evident in 1972 and 1973. Again the cause could lie with the model's failure to produce higher algal peaks during August, thus producing an inadequate food supply for the copepods. The same problem appears to exist for the model cladoceran population (Figures 26 and 12).

Observed quarterly means for variables used in the simulation model are presented in Tables A1-A9 of the Appendix.

HYDRODYNAMIC CONSIDERATIONS

It is clear from the water retention time (566 days) that advection plays a dominant role in the dynamic aspects of Kootenay Lake. Figure 27 is indicative of the flow of the Kootenay River at its point of entrance into the lake. During periods of peak volume flow, the velocity of the river reaches approximately one meter per second. If the river continued up the lake as a slug of water, it would move over 600 kilometers in one week. Conversely, if mixing were complete, a corresponding input of 1,500 cubic meters per second would displace one-fortieth of the lake's volume in one week. Since the lake is on the order of one hundred kilometers long, this would suggest a weekly movement of about two and a half kilometers. Obviously, the true value lies somewhere between these two extremes. Because velocity measurements were not made during much of the study (then only at Station 2), the model used the lower bound to calculate expected velocities at each point. This approach required use of a vertical transfer coefficient

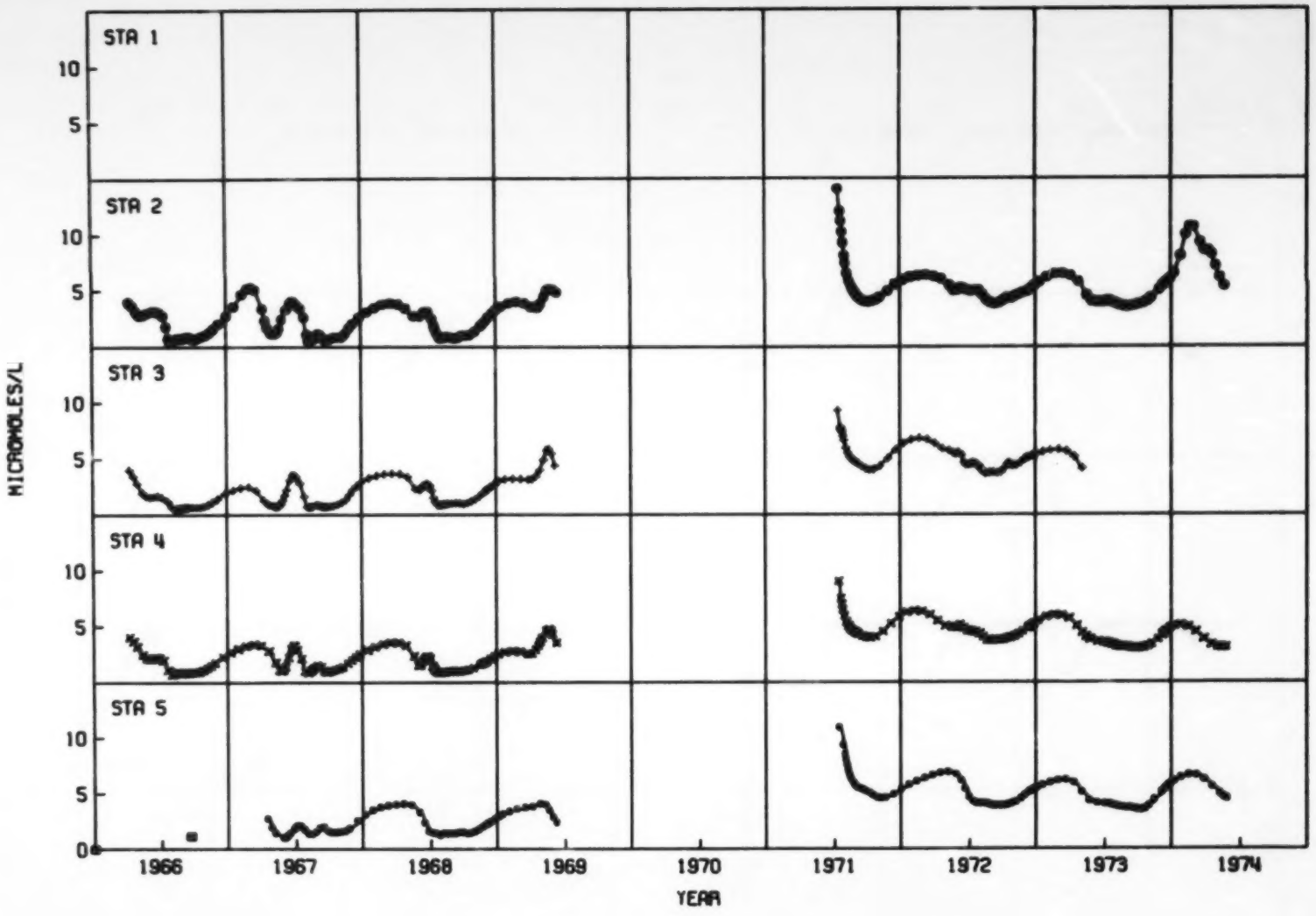

Figure 23. Simulated ammonium concentrations.

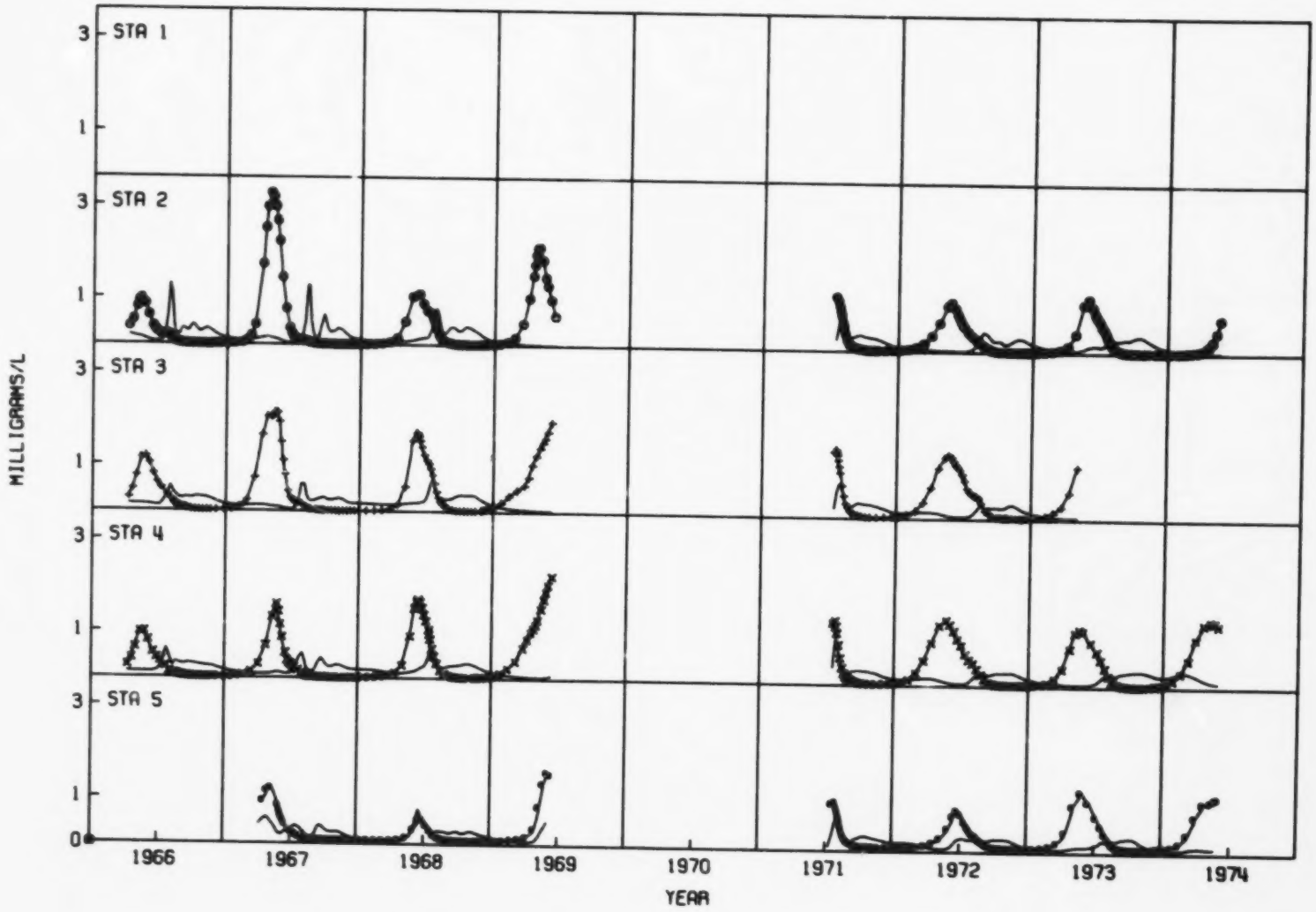

Figure 24. Simulated phytoplankton levels.

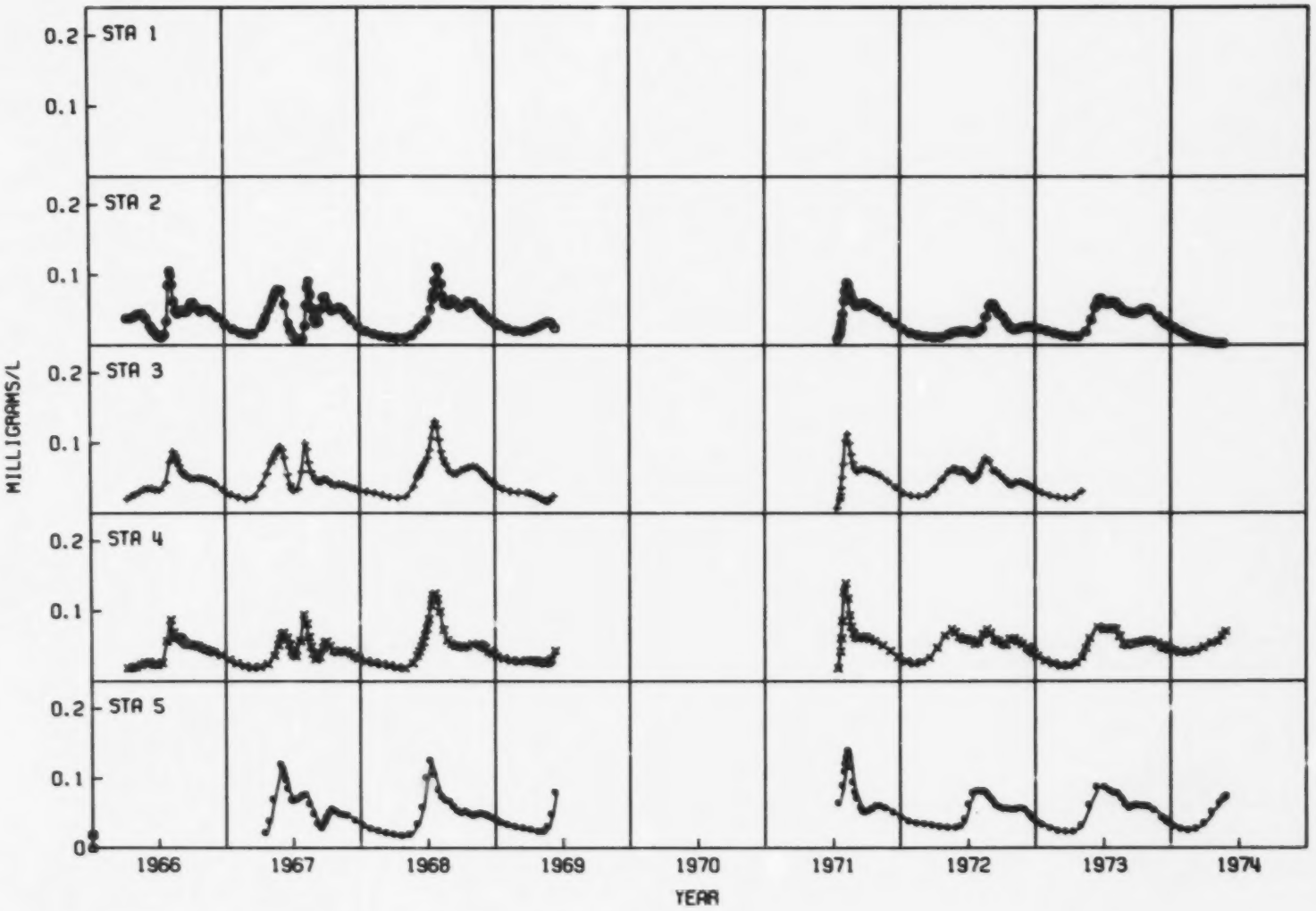

Figure 25. Simulated copepod levels.

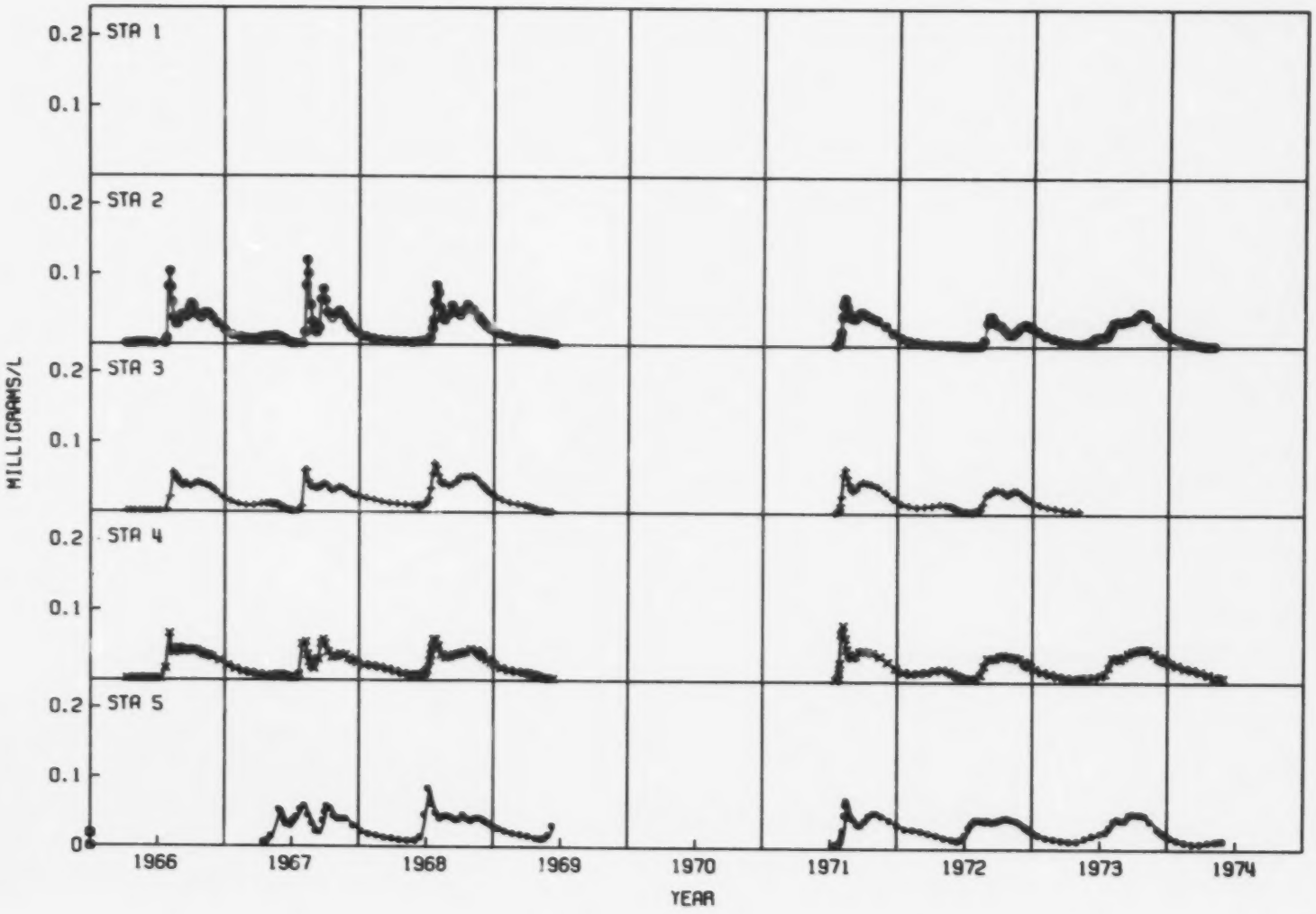

Figure 26. Simulated cladoceran levels.

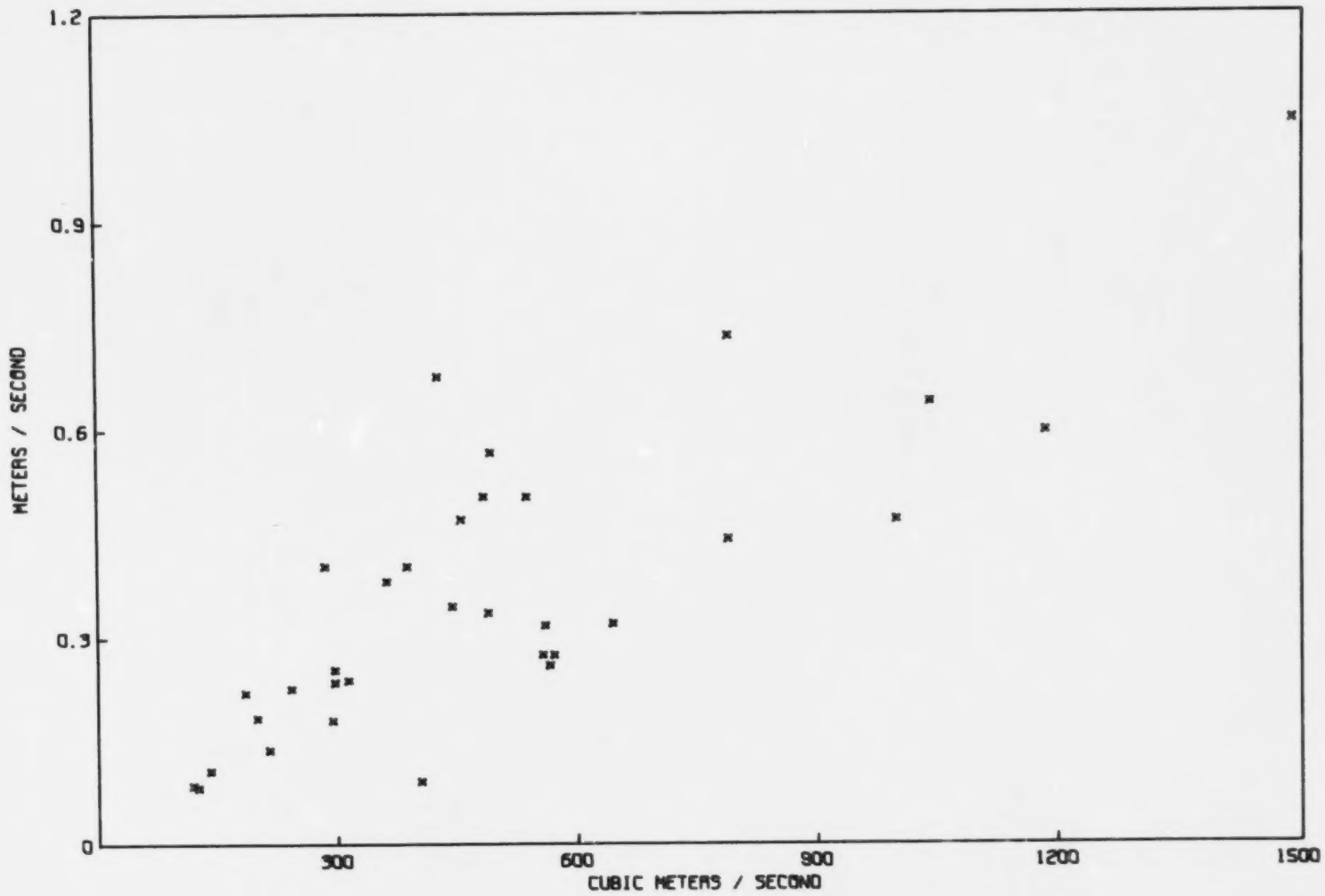

Figure 27. Velocity and volume flow at Station 1.

of approximately 0.15 cm wk^{-1} x 10^3, even though studies of some lakes (Jassby and Powell[40]) suggest that this value may be low by an order of magnitude; molecular transfer is approximately 0.07 cm wk^{-1} x 10^3.

In order to establish the actual velocities existing in the lake under different river flows, two additional sampling stations were established near Station 2. The first was located midway between Station 2 and the west bank, and the second was located midway between Station 2 and the east bank. Drogue measurements were made at one, five, and ten meters (occasionally at twenty meters) at Station 2 as well as at the two new stations. Figure 28 presents the results of these measurements for nine days during 1974-75. These have been ordered according to river flow in an attempt to focus on patterns of horizontal flow in the vicinity of Station 2. Recalling that the main axis of the lake lies in a north-northwest south-southeast direction, it is apparent at once that the turbulent motion in the lake is extreme. Only occasionally are the directions of flow at the three or four sampling depths coincident, although the magnitudes are similar. A further consolidation of the results is presented in Figure 29. Clearly the mean northward flow is not coupled strongly with input volume. There is, however, evidence to support a counterclockwise motion in the lake, that is, the river water flows more strongly along the east shore and returns to some extent along the west shore. This provides for little motion in the center where Station 2 is located. Examination of these results point to a rather haphazard relationship between velocity and volume flow at Station 2, and at other times southward flow occurs. In the model, of course, southward flow was never permitted since the river waters were always presumed to contribute to a northward displacement. Actual measurements during periods of high flow (greater than 1,500 cubic meters per second) suggest a northward flow at Station 2 of about 0.2 meters per second, approximately ten times more than that calculated by volume displacement. More realism can be expected in the model if the velocity component is modified accordingly, and the vertical transfer coefficient changed as well.

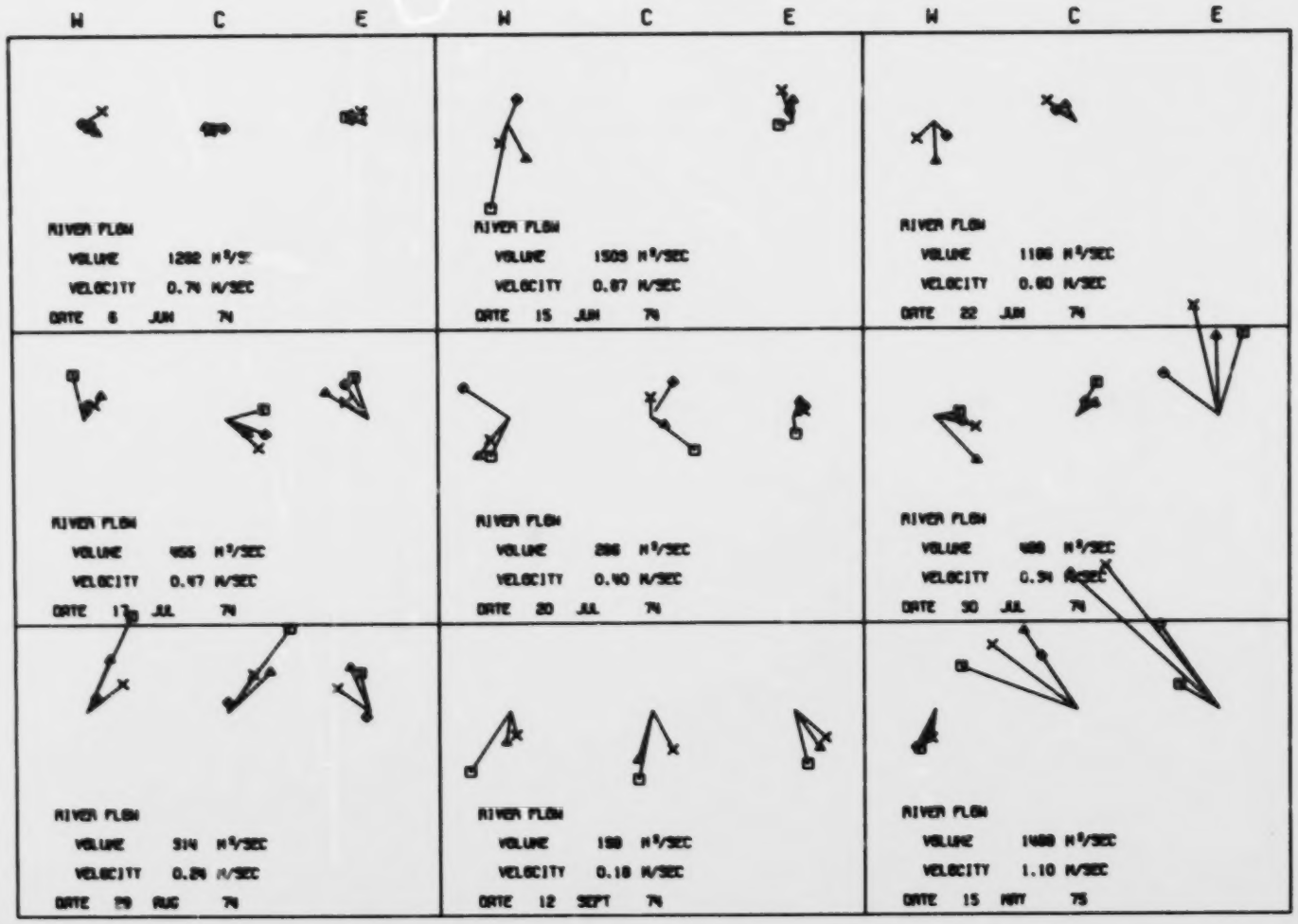

Figure 28. Velocity at four depths at Station 2.

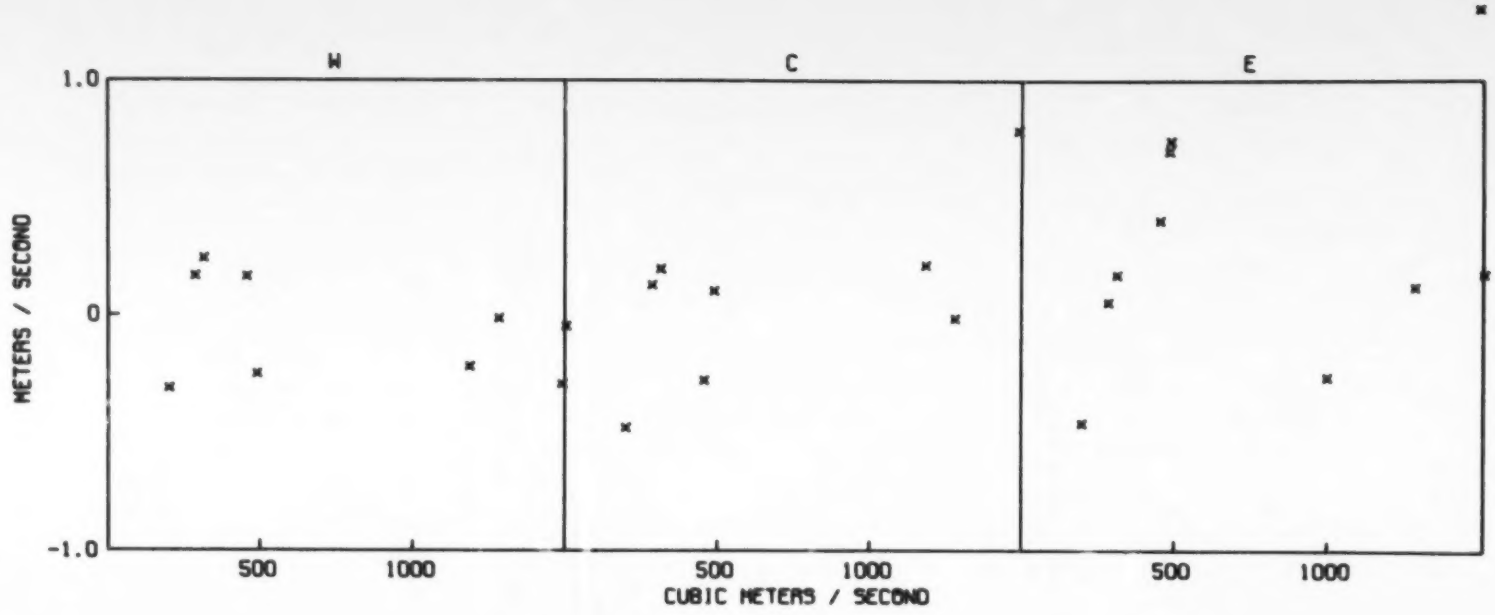

Figure 29. Mean northerly velocity at Station 2 along north-south axis of lake, and flow at Station 1.

SECTION VI

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SECTION VII

APPENDIX

OBSERVED QUARTERLY MEANS FOR KOOTENAY LAKE VARIABLES USED IN SIMULATION MODEL

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Table A-1. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) FOR KOOTENAY RIVER FLOW (m^3/sec) AT STATION 1

Qtr.	Year							
	1966	1967	1968	1969	1971	1972	1973	1974
1		207(1)	165(3)	143(2)			140(3)	842(2)
2	1300(4)	1659(4)	1245(4)	1668(3)		899(5)	247(6)	1344(4)
3	366(7)	579(8)	507(8)		484(12)	657(13)	326(10)	
4	139(3)	163(4)	249(4)		158(2)	729(4)	376(4)	

Table A-2. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF TEMPERATURE AT 1 M (STATION 1) AND MEAN TEMPERATURE OVER 10 M (STATIONS 2-5)

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
1	1		1.5(1)	3.4(3)	1.5(1)			0.8(2)	1.6(1)
	2	8.6(4)	10.2(4)	8.0(4)	6.5(3)		8.7(5)	11.2(5)	8.2(3)
	3	17.7(9)	17.5(4)	16.8(8)		17.2(11)	15.2(12)	17.2(8)	
	4	9.9(5)	11.6(4)	5.5(4)		5.2(2)	11.4(4)	7.4(2)	
2	1		5.3(2)		2.8(1)			3.2(2)	2.2(1)
	2	7.2(4)	8.7(5)	7.9(3)	6.9(3)		7.2(5)	9.1(5)	6.6(3)
	3	16.9(10)	16.4(4)	16.4(8)		15.7(12)	15.5(12)	17.6(8)	
	4	11.6(5)	13.9(4)	8.3(4)		9.7(2)	9.9(4)	8.2(2)	
3	1		5.1(2)	3.4(2)	2.8(2)			3.9(3)	
	2	7.4(4)	9.0(5)	8.0(4)	7.0(3)		7.3(5)	5.8(3)	
	3	17.4(8)	17.2(4)	16.3(7)		16.5(10)	15.5(13)		
	4	12.7(4)	11.3(4)	7.3(3)		10.5(2)	10.6(4)		
4	1		5.1(3)	4.3(1)	2.3(1)			3.6(2)	1.8(1)
	2	7.6(4)	9.1(5)	7.8(4)	7.2(3)		7.7(5)	9.5(5)	7.4(3)
	3	17.3(9)	17.2(5)	16.4(7)		16.7(10)	15.6(13)	17.3(8)	
	4	13.0(4)	14.9(3)	7.9(3)		10.5(2)	11.3(4)	10.0(3)	
5	1			3.2(3)	2.6(2)			3.4(1)	
	2		11.1(2)	8.8(4)	8.4(3)		7.6(3)	11.8(3)	9.9(2)
	3		17.3(5)	16.6(8)		17.0(10)	15.7(11)	17.1(8)	
	4		14.6(4)	11.2(4)		13.1(1)	10.6(3)		

Table A-3. QUARTERLY MEANS (NUMBERS OF OBSERVATIONS) OF THE EXTINCTION COEFFICIENT (CORRECTED FOR ALGAL CONTENT) OVER 5 M AT STATION 1 AND OVER 10 M AT STATIONS 2-5

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
1	1		1.10(1)	1.75(3)	1.54(2)			1.32(2)	2.58(2)
	2	1.92(2)	3.13(4)	2.05(2)	1.93(3)		1.90(5)	1.32(6)	2.56(4)
	3	0.84(9)	0.98(8)	0.87(8)		0.70(11)	1.20(12)	1.21(8)	
	4	0.85(9)	0.52(4)	0.67(3)		0.79(2)	0.69(4)	1.75(2)	
2	1		0.30(2)		0.23(1)			0.23(2)	0.36(2)
	2	1.16(4)	1.15(6)	0.92(3)	1.01(3)		0.37(5)	0.32(5)	0.33(4)
	3	0.25(10)	0.70(8)	0.36(8)		0.34(12)	0.42(12)	0.40(8)	
	4	0.17(5)	0.29(4)	0.18(4)		0.20(2)	0.29(4)	0.31(2)	
3	1		0.23(2)	0.17(2)				0.24(3)	
	2	0.74(4)	0.73(6)	0.63(4)	1.10(2)		0.36(5)	0.24(3)	
	3	0.28(8)	0.58(8)	0.33(7)		0.31(10)	0.41(13)		
	4	0.23(4)	0.42(4)	0.18(3)		0.21(2)	0.39(3)		
4	1		0.16(3)	0.10(1)	0.15(1)			0.24(2)	0.27(2)
	2	0.56(3)	0.60(6)	0.47(4)	0.91(2)		0.34(5)	0.40(5)	0.35(4)
	3	0.34(9)	0.57(8)	0.32(7)		0.32(10)	0.42(13)	0.34(8)	
	4	0.24(4)	0.26(3)	0.18(3)		0.18(2)	0.28(3)	0.22(2)	
5	1			0.25(3)	0.09(2)			0.22(1)	
	2		0.46(3)	0.34(4)	0.60(2)		0.26(3)	0.33(3)	
	3		0.56(8)	0.27(8)		0.27(10)	0.37(11)	0.34(8)	
	4		0.25(4)	0.15(4)		0.16(1)	0.24(3)	0.22(2)	

Table A-4. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF INORGANIC PHOSPHATE AS µM/L AT 1 M (STATION 1) AND MEAN INORGANIC PHOSPHATE OVER 10 M (STATIONS 2-5)

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
1	1		12.28(1)	9.02(3)	4.73(2)			1.27(2)	0.36(2)
	2	4.01(4)	2.58(5)	3.65(4)	0.86(3)		0.13(5)	0.48(5)	0.24(4)
	3	7.70(9)	4.28(8)	5.64(8)		0.66(11)	0.07(12)	0.26(8)	
	4	11.54(5)	11.01(4)	3.38(4)		1.23(2)	0.25(4)	0.47(2)	
2	1		2.85(2)		3.04(1)			0.60(2)	0.48(2)
	2	1.54(4)	2.40(6)	2.66(3)	1.93(3)		0.50(5)	0.12(5)	0.32(4)
	3	3.38(10)	1.62(8)	3.02(8)		0.40(12)	0.06(12)	0.05(8)	
	4	3.00(5)	2.17(4)	2.77(4)		0.32(2)	0.32(4)	0.36(2)	
3	1		2.78(2)	2.91(2)	2.75(2)			0.55(3)	
	2	1.62(4)	2.29(6)	2.65(4)	1.79(3)		0.48(5)	0.28(3)	
	3	3.19(8)	1.16(8)	2.63(7)		0.39(10)	0.03(13)		
	4	2.73(4)	1.99(4)	2.57(3)		0.38(2)	0.16(4)		
4	1		2.41(3)	2.56(1)	2.93(1)			0.54(2)	0.42(2)
	2	1.80(4)	2.16(6)	2.55(4)	1.92(3)		0.57(5)	0.13(5)	0.29(4)
	3	2.54(9)	0.94(8)	2.37(7)		0.38(10)	0.03(13)	0.03(5)	
	4	2.14(4)	1.27(3)	2.40(3)		0.47(2)	0.12(4)	0.18(3)	
5	1			2.18(3)	2.45(2)			0.30(1)	
	2		1.21(3)	1.55(4)	1.60(3)		0.50(3)	0.03(3)	
	3		0.51(8)	1.67(8)		0.27(10)	0.01(11)	0.02(8)	
	4		0.66(4)	1.90(4)		0.00(1)	0.10(3)	0.04(2)	

Table A-5. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF NITRATE CONCENTRATION AS µM/L AT 1 M (STATION 1) AND MEAN NITRATE CONCENTRATION OVER 10 M (STATIONS 2-5)

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
1	1		31.36(1)	7.93(3)	8.71(2)			8.38(2)	17.14(2)
	2		8.36(5)	5.45(4)	8.36(3)		6.09(5)	2.90(6)	6.64(4)
	3	1.10(6)	1.88(8)	3.70(8)		5.44(11)	3.39(12)	4.16(8)	
	4	1.20(5)	2.14(4)	4.75(4)		3.03(2)	3.67(4)	5.99(2)	
2	1		3.57(2)		7.71(1)			7.66(2)	8.62(2)
	2		4.48(6)	5.31(3)	7.52(3)		8.06(5)	2.70(5)	6.09(4)
	3	1.27(8)	2.07(8)	3.74(8)		6.24(12)	3.17(12)	3.73(8)	
	4	1.67(5)	3.36(4)	4.67(4)		5.82(2)	4.95(4)	5.92(2)	
3	1		3.71(2)	7.50(2)	6.85(2)			7.95(3)	
	2		3.69(6)	4.45(4)	7.83(3)		7.31(5)	4.13(3)	
	3	1.56(7)	2.07(8)	3.98(7)		5.71(10)	2.91(13)		
	4	1.36(4)	3.79(4)	4.60(3)		4.72(2)	3.75(4)		
4	1		3.38(3)	5.00(1)	7.57(1)			7.59(2)	8.71(2)
	2		3.01(6)	3.98(4)	7.24(3)		7.33(5)	3.42(5)	5.44(4)
	3	1.38(8)	1.99(8)	3.62(7)		5.70(10)	2.86(13)	3.28(7)	
	4	1.43(4)	2.62(3)	4.02(3)		3.79(2)	4.02(4)	4.10(3)	
5	1			6.05(3)	7.07(2)			6.28(1)	
	2		1.79(3)	2.53(4)	6.26(3)		5.48(3)	1.79(3)	
	3		2.02(8)	3.63(8)		4.46(10)	2.36(11)	2.96(8)	
	4		3.05(4)	4.09(4)		0.99(1)	4.40(3)	3.94(2)	

Table A-6. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF AMMONIUM CONCENTRATION AS μM/L AT 1 M (STATION 1) AND MEAN AMMONIUM CONCENTRATION OVER 10 M (STATIONS 2-5)

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
1	1			8.16(3)	6.03(2)			6.00(2)	1.95(2)
	2			2.61(2)	1.43(3)		1.91(5)	1.97(6)	3.55(4)
	3		6.56(1)	2.99(3)		5.55(11)	1.47(12)	1.65(8)	
	4		4.83(2)	12.35(4)		0.90(2)	2.19(4)	3.25(2)	
2	1				4.02(1)			4.53(2)	1.40(2)
	2		0.82(2)	1.69(3)	1.41(3)		1.61(5)	2.14(5)	1.65(4)
	3		2.34(5)	1.03(7)		3.59(12)	1.14(12)	1.34(8)	
	4		2.99(4)	7.51(4)		0.91(2)	2.27(4)	1.18(2)	
3	1			1.06(1)	7.40(2)			2.62(3)	
	2		0.42(2)	2.93(4)	1.03(3)		1.85(5)	2.24(3)	
	3		1.82(6)	1.52(4)		4.50(10)	1.34(13)		
	4		1.82(2)	8.30(3)		0.72(2)	2.18(4)		
4	1			0.14(1)	2.19(1)			6.57(2)	1.59(2)
	2		2.71(3)	1.66(4)	1.37(3)		1.54(5)	2.21(5)	1.78(4)
	3		1.47(7)	1.48(5)		4.90(10)	1.79(13)	1.32(7)	
	4		4.20(3)	7.81(3)		0.77(2)	2.05(4)	1.11(3)	
5	1			0.61(3)	8.64(2)			5.10(1)	
	2		3.03(3)	1.94(4)	1.41(3)		1.25(3)	2.08(3)	
	3		3.35(5)	0.76(5)		3.16(10)	1.55(11)	1.24(8)	
	4		1.39(4)	7.81(4)		1.02(1)	2.41(3)	1.33(2)	

Table A-7. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF MEAN PHYTOPLANKTON DENSITY OVER 10 M AS mg/L (STATIONS 2-5)

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
2	1		0.20(1)		0.05(1)			0.17(2)	0.20(2)
	2	0.64(4)	0.90(6)	0.90(3)	1.42(3)		0.58(5)	1.00(5)	0.63(4)
	3	1.30(10)	0.61(8)	0.77(8)		0.77(12)	0.76(12)	0.73(8)	
	4	0.42(5)	0.60(4)	0.79(4)		0.67(2)	0.37(4)	0.32(2)	
3	1		0.10(1)	0.42(2)	0.75(2)			0.30(3)	
	2	0.26(4)	0.54(5)	0.96(4)	1.52(3)		0.53(5)	0.85(3)	
	3	1.14(8)	0.41(8)	0.59(6)		1.31(10)	0.79(13)		
	4	0.36	0.61(4)	0.83(3)		0.55(2)	0.47(4)		
4	1		0.70(1)	0.55(1)	0.50(1)			0.32(2)	0.30(2)
	2	0.22(4)	0.60(4)	0.81(4)	1.32(3)		0.37(5)	0.75(5)	0.87(4)
	3	0.87(9)	0.46(8)	0.58(6)		0.86(10)	0.87(13)	0.53(7)	
	4	1.00(4)	0.45(3)	0.98(3)		0.73(2)	0.43(4)	0.49(3)	
5	1			0.47(3)	0.90(2)			0.35(1)	
	2		0.35(3)	0.88(4)	1.68(3)		0.68(3)	0.73(3)	
	3		0.49(8)	0.57(7)		1.08(10)	0.93(11)	0.38(8)	
	4		0.54(4)	0.71(4)		1.48(1)	0.54(3)	0.58(2)	

Table A-8. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF MEAN COPEPOD DENSITY OVER 10 M AS mg/L (STATIONS 2-5)

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
2	1		0.008(2)		0.002(1)			0.014(2)	0.014(2)
	2	0.017(3)	0.039(6)	0.014(3)	0.002(1)		0.018(4)	0.107(5)	0.005(4)
	3	0.033(9)	0.075(8)	0.068(7)		0.066(11)	0.076(12)	0.155(7)	
	4	0.029(4)	0.046(4)	0.050(4)		0.054(2)	0.025(4)	0.013(2)	
3	1		0.013(1)	0.007(2)	0.009(2)			0.018(3)	
	2	0.007(3)	0.030(6)	0.018(4)	0.005(3)		0.008(5)	0.018(2)	
	3	0.041(7)	0.076(8)	0.067(6)		0.068(10)	0.077(13)		
	4	0.636(3)	0.035(4)	0.038(3)		0.073(2)	0.066(4)		
4	1		0.010(3)	0.006(1)	0.026(1)			0.018(2)	0.031(2)
	2	0.013(3)	0.041(6)	0.054(4)	0.004(3)		0.018(4)	0.049(5)	0.014(4)
	3	0.063(9)	0.057(8)	0.111(6)		0.083(9)	0.084(13)	0.119(6)	
	4	0.037(3)	0.044(3)	0.045(3)		0.042(2)	0.050(4)	0.030(3)	
5	1							0.007(1)	
	2		0.034(3)	0.062(3)	0.021(3)		0.010(3)	0.049(2)	
	3		0.099(8)	0.109(8)		0.154(10)	0.076(10)	0.096(6)	
	4		0.45(4)	0.044(4)		0.130(1)	0.050(3)	0.098(2)	

Table A-9. QUARTERLY MEANS (NUMBER OF OBSERVATIONS) OF MEAN CLADOCERAN DENSITY OVER 10 M AS mg/L (STATIONS 2-5).

Sta.	Qtr.	Year							
		1966	1967	1968	1969	1971	1972	1973	1974
2	1		0.000(2)		0.000(1)			0.000(2)	0.000(2)
	2	0.000(3)	0.000(6)	0.000(3)	0.000(3)		0.000(4)	0.000(5)	0.000(4)
	3	0.026(9)	0.060(8)	0.038(7)		0.015(11)	0.016(12)	0.070(7)	
	4	0.002(4)	0.048(4)	0.010(4)		0.004(2)	0.001(4)	0.004(2)	
3	1		0.000(1)	0.000(2)	0.000(2)			0.000(3)	
	2	0.000(3)	0.000(6)	0.000(4)	0.000(3)		0.000(5)	0.000(2)	
	3	0.035(7)	0.036(8)	0.020(6)		0.012(10)	0.010(13)		
	4	0.004(3)	0.029(4)	0.001(3)		0.005(2)	0.007(4)		
4	1		0.000(3)	0.000(1)	0.000(1)			0.000(2)	0.000(2)
	2	0.000(3)	0.000(6)	0.000(4)	0.000(3)		0.000(4)	0.000(5)	0.000(4)
	3	0.024(9)	0.050(8)	0.015(6)		0.014(9)	0.009(13)	0.063(6)	
	4	0.003(3)	0.044(3)	0.001(3)		0.003(2)	0.007(4)	0.008(3)	
5	1							0.000(1)	
	2		0.000(3)	0.000(3)	0.000(3)		0.000(3)	0.000(2)	
	3		0.043(8)	0.010(8)		0.020(10)	0.009(10)	0.026(6)	
	4		0.011(4)	0.001(4)		0.007(1)	0.001(3)	0.036(2)	